ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE

Vol. 64

No. 4

2000

ISSN 1211-376X

ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE[1]

Acta Soc. Zool. Bohem. Vol. 64, No. 4 issued 2000 December 29

ISSN 1211-376X 47678

Editor: Karel Hůrka
Executive editor: David Král

Editorial board: Petr Benda, Jan Buchar, Ivo Hodek, Alois Honěk, Jaroslav Hrbáček, Vojtěch Jarošík, František Moravec, Josef Rusek, Jiří Vávra, Jan Zima

Published and distributed by the Czech Zoological Society

Orders should be sent to the Czech Zoological Society, Viničná 7, CZ–128 00 Praha 2, Czech Republic

All foreign orders are executed by agency Kubon-Sagner, Buch Export-Import GmbH, D–80328 Munchen, BRD (fax ++(089)54218–218, e-mail: postmaster@kubon-sagner.de), or by agency Myris Trade Ltd., PO Box 2, CZ–142 01 Praha, Czech Republic (tel. ++4202/4752774, fax ++4202/496595, e-mail myris@login.cz). The foreign orders executed by other subscription agencies contradict the publisher's agreements with the above mentioned sole agencies and they are distributed illegally.

Print by Price Print Service, Praha, Czech Republic.

Annual subscription (Volume 64, 2000, 4 issues)

Institutional subscription:	Europe:	USD 80.00
	Other countries:	USD 90.00
Private subscription:	Europe:	USD 40.00
	Other countries:	USD 50 00

This issue was supported by Czech Ministry of Education (MŠMT ČR) and the Český literární fond (Czech Literary Foundation).

© Czech Zoological Society, Praha, 2000

---

[1] A direct continuation of:
(i) Vol. 1 (1927–1932). Zpráva o činnosti československé zoologické společnosti za léta 1927–1932
(ii) Vol. 2–53 (1933–1989): Věstník československé společnosti zoologické (*Věst. Čs. Společ. Zool.*)
(iii) Vol. 54–56 (1990–1992) Acta Societatis Zoologicae Bohemoslovacae (*Acta Soc. Zool. Bohemoslov.*)

Acta Soc. Zool. Bohem. **64**: 331–398, 2000
ISSN 1211-376X

Taxonomic revision of *Myotis mystacinus* group (Mammalia: Chiroptera) in the western Palearctic*

Petr BENDA[1] & Katerina A. TSYTSULINA[2]

[1] Department of Zoology, National Museum (Natural History), Václavské náměstí 68,
CZ–115 79 Praha 1, Czech Republic; e-mail: petr.benda@nm.cz
[2] Institute of Zoology, Russian Academy of Sciences, Universitetskaja nabereznaja 1,
Saint Petersburg, RU–199034, Russia

Received August 27, 2000; accepted October 5, 2000
Published December 29, 2000

Abstract. We restudied the systematic arrangement of the *Myotis mystacinus* group in the western part of the Palearctic region (Europe, North Africa, and Caucasus region) using morphometry of the skull and wings, and morphology of teeth and bacula in more than 650 museum specimens. In the stated region we recognized five species with several subspecies. *Myotis brandtii brandtii* (Eversmann, 1845), which occurs in central and north-eastern Europe, the Balkans and the Caucasus region; *Myotis mystacinus mystacinus* (Kuhl, 1817), which occurs in the European mixed forests from Ireland and the Balkans to the Ural Mts., *M. m. occidentalis* Benda ssp. n., which occurs in the western Mediterranean, *M. m. caucasicus* Tsytsulina ssp. n., which occurs in the Caucasus Mts., Transcaucasia, and Armenian Highlands; and *Myotis aurascens* Kusjakin, 1935 stat. n., which occurs in south-eastern Europe from northern Italy, Dalmatia and the Balkans through the steppes of southern Ukraine and Ciscaucasia to Transcaucasia and the steppes of western Kazakhstan (this form probably occurs in Asia Minor as well). The Sevan Lake basin in Armenia is inhabited by an endemic form, *Myotis hajastanicus* Argyropulo, 1939 stat. n. In the north-eastern part of the Middle East (eastern Turkey, eastern Transcaucasia, Iran) and more to the east another form occurs, tentatively identified here as *Myotis nipalensis transcaspicus* Ogneff et Heptner, 1928 stat. n. The paper includes revised diagnoses of all newly defined taxa.

Taxonomy, Chiroptera, *Myotis mystacinus*, *Myotis brandtii*, *Myotis aurascens*, *Myotis hajastanicus*, *Myotis nipalensis*, Palearctic region, Europe, the Balkans, Caucasus Mts.

INTRODUCTION

The *Myotis mystacinus* group (whiskered bats) is composed of several species inhabiting the Palearctic and the Oriental regions (Pavlinov et al. 1995). The group belongs to the subgenus *Selysius* Bonaparte, 1841, which was characterized by Tate (1941) as follows: "with small feet, length about 50 per cent of tibia, wing to base of toe, calcar usually with lobe, ear small, rostrum low, frontal region rising rather abruptly". The type species of this subgenus is *Myotis mystacinus* (Kuhl, 1817).

Tate (1941) divided the subgenus *Selysius* in the following five groups, viz. *mystacinus*, *ater*, *emarginatus*, and *siligorensis* sections, and a section of (four) species incertae sedis. Members of the Tate's (1941) *mystacinus* section were characterized as "relatively unspecialized, of quite small size". This section included a total of 27 taxa, incl. 11 valid species and 17 synonyms of the species *M. mystacinus* (viz. *brandtii*, *gracilis*, *sibiricus*, *ikonnikovi*, *sogdianus*, *przewalskii*, *pamirensis*, *transcaspicus*, *kukunorensis*, *nipalensis*, *meinertzhageni*, *montivagus*, *muricola*, *moupinensis*,

---

*Dedicated to our great teachers, Prof. Dr. Vladimír Hanák (Prague) and Dr. Petr Petrovič Strelkov (St. Petersburg), on the occasion their forthcoming seventies anniversaries.

orii, *caliginosus*, and *blanfordi*). All of these synonymized names (but *moupinensis* and *orii*) apply to bats from the Palearctic region and from the part of the Oriental region adjacent to the Palearctic region. Ellerman & Morrison-Scott (1951) considered these forms as subspecies (13 in total) or as synonyms of *M. mystacinus*, recognizing as valid at the species level only *M. ikonnikovi* Ognev, 1911, which occurs in the north-eastern Asia. In addition to Tate (1941) they recognized the subspecies *aurascens*, *bulgaricus* and *hajastanicus*. In summary, Ellerman & Morrison-Scott (1951) divided whiskered bats of the Palearctic in two species: *M. mystacinus* with 17 subspecies and several synonyms, and the monotypic *M. ikonnikovi*.

In the western Palearctic (here understood as Europe, North Africa, and the Middle East, incl. the Caucasus and Caspian regions, see Figs. 1, 2) Ellerman & Morrison-Scott (1951) recognized five taxa of the *M. mystacinus* group. All of them were included in the nominotypical species *Myotis mystacinus mystacinus* (occurs in Europe), *M. m. brandtii* (Eversmann, 1845) (Ural Mts. and Siberia), *M. m. aurascens* Kusjakin, 1935 (Northern Caucasus Mts.), *M. m. bulgaricus* Heinrich, 1936 (Bulgaria), and *M. m. hajastanicus* Argyropulo, 1939 (Armenia). Abelencev et al. (1956) distinguished eight subspecies of *M. mystacinus*, incl. three in the western Palearctic: *M. m. mystacinus* (western Europe), *M. m. brandtii* (eastern Europe and Siberia), and *M. m. aurascens* (Crimea, Caucasus Mts. and the steppes of Ukraine), and five forms in the eastern part of the distribution range of the species (*gracilis*, *transcaspicus*, *przewalskii*, *pamirensis*, and *kukunorensis*).

The subspecific identity of the western Palearctic populations assigned to *M. mystacinus* was for the first time studied by Hanák (1965). In addition to the recognition of *M. brandtii* from central and eastern Europe as an independent species (see below), he commented also on the records of *M. ikonnikovi* from the south-eastern Europe (see Abelencev 1950, Kvartirnikov 1957, Dumitrescu et al. 1963). He regarded them as small individuals of *M. m. mystacinus*. In addition, he revised *M. m. bulgaricus* Heinrich, 1936, concluding that this is a junior synonym of *M. m. mystacinus*, and separated the populations of Crimea and the Caucasus Mts. from both the nominotypical form and from *brandtii* (though not applying any name to them). Also, he defined the well distinguishable forms from the Central and Middle Asia: *M. m. transcaspicus* Ogneff et Heptner, 1928 (lowlands of Central Asia), *M. m. przewalskii* Bobrinskoj, 1926 (deserts of western China and southern Mongolia), and an unnamed mountain form.

Hanak's (1965) results were followed by Stubbe & Chotolchu (1968). They divided the Palearctic members of *M. mystacinus* s. l. based on the morphology of teeth and baculum in three "groups": (1) *mystacinus*-group, found only in Germany, (2) *brandtii*-group, found in eastern Europe and northern Asia from Slovakia to Siberia and the Far East, and (3) *przewalskii*-group, found in southern part of the Palearctic, from the Balkans, through Crimea and the Caucasus Mts. to Central Asia and Mongolia. However, they did not elevate these "groups" to the species rank, recognizing them as the subspecies *Myotis mystacinus brandtii* and *M. "mystacinus" przewalskii* (both limited to Mongolia). Regardless of this conclusion, Corbet (1978) recognized in the western Palearctic ("Europe and western Asia") only *M. m. mystacinus* and *M. brandtii*.

In short, *M. brandtii* (Eversmann, 1845) was recognized as a separate taxon in the western Palearctic on the basis of baculum (= os penis) characters (Topál 1958, Hanak 1965, Vlček 1970), and of cranial and dental characters (Hanak 1965, 1970, 1971, Gauckler & Kraus 1970). Hanak (1965) listed as characters distinguishing *M. brandtii* and *M. mystacinus* (recognized by him as subspecies): absolute size (particularly longitudinal dimensions of the skull), shape of the whole penis, and the structure of os penis. Stubbe & Chotolchu (1968), Gauckler & Kraus (1970), Hanak (1970, 1971), Tupinier & Aellen (1978), and Menu & Popelard (1987) described several distinguishing characters on the premolars and molars: relative size of the first two premolars in both jaws (P^2P^3 and P_2P_3), height of the mesiopalatal cingular cusp on the third upper premolar (P^4) and the presence and/or development of additional cusps and crests on the occlusion surface of molars All of these structures are well developed in *M brandtii*, while they are often absent in *M mystacinus* Following these studies it started to be accepted, that *M brandtii* occurs in central Europe (Gauckler & Kraus 1970, Hanak 1970, 1971, Walter 1972, Ruprecht 1974, Roer 1974), in the western Europe (Hanak 1970, Tupinier & Aellen 1978, Fairon 1980), in Scandinavia (Egsbaek et al 1971, Baagøe 1973), in eastern Europe and northern Asia (Fedorov 1978, Buša 1980, Strelkov & Buntova 1982, Strelkov 1983a, b), in the Balkans (Horaček et al 1974), and in the Caucasus region (Strelkov 1983a, b, Albayrak 1991) These characters were revised by Hackethal (1982) using material from Germany, and by Strelkov & Buntova (1982) and Strelkov (1983b) using material from most parts of the Palearctic In addition, Rybař (1976) observed that the angle between the roots on the buccal side of P^4 from the mesial direction is different in the two forms (the angle being sharper in *M brandtii*) Strelkov & Buntova (1982) confirmed the validity of this character, albeit with reservations

Strelkov & Buntova (1982) and Strelkov (1983a) performed morphometrical studies of skull, teeth and baculum of over 550 specimens of *M mystacinus* and *M brandtii*, using specimens from the territory of the former USSR (and adjacent areas) From this area, they determined and described occurrence of both species, *M mystacinus* and *M brandtii* Strelkov (1983a) recognized in the western Palearctic (i e , European Russia, Baltic States, Belorussia, Ukraine, Moldavia, and Caucasus region) *M brandtii* as a species of low morphological variation, referring all other respective populations to *M mystacinus* (referring only the populations from eastern Siberia and the Far East to *M b gracilis* Ognev, 1927) He believed, that *M mystacinus* is a very variable form, and recognized from the western Palearctic the following three forms (1) *M m mystacinus*, which occurs in the boreal zone of Europe (Baltic countries, Belorussia, Ural Mts), (2) a forest form of North Caucasus Mts and Transcaucasia, named *M m aurascens*, and (3) a steppe form occurring in Moldavia, southern Ukraine, Crimea, and the lowlands of Ciscaucasia, which he newly described as *M m popovi* Strelkov, 1983 East populations inhabiting the area of Central Asia to Mongolia he attributed to a single form, *M m przewalskii* (the easternmost population of this complex was later described as *M m mongolicus* Kruskop et Borissenko, 1996) Later, Strelkov (1989) continued his studies of baculum, which led him to propose that the *M mystacinus* populations of Ural Mts and the Samara region (middle Volga river) are different from other *mystacinus* populations, without selecting a name for the form

Helversen (1989a), following Stubbe & Chotolchu (1968), mentioned *M mystacinus* from Asia Minor under the names *M (mystacinus) przewalskii* or *M przewalskii* He explained, that "The baculum of *przewalskii* is so different from the tiny baculum of *mystacinus* (in addition to differences in skull, chromosomes and ecology) that this third form [in addition to *mystacinus* s s and *brandtii*] should be regarded as a good species ", without adding any further explanation Albayrak (1991) studied the Turkish populations of *M mystacinus* and compared them with the published data (i e Hanak 1970, Gauckler & Kraus 1970) also came to the conclusion that the nominotypic subspecies does not occur in Turkey, and attributed all his records to *M m hajastanicus*

Helversen (1989b) recognized in Europe four forms from the *M mystacinus* group, giving to all of them the species rank In addition to *M mystacinus* and *M brandtii*, he mentioned *M ikonnikovi* and *M przewalskii* *Myotis ikonnikovi* ("or up-to-present unknown form") he described as follows "very small (FA < 32 mm), ears light and short, tragus scarcely overtops a notch on the posterior ear margin, (so far, there are known only two individuals from Greece)" [our translation from German] On *M przewalskii* he wrote "In the eastern Mediterranean (southern Yugoslavia and Greece, perhaps also farther to the west) a particularly slender whiskered bat occurs, which can be – on the basis of the morphology of baculum considered as an independent species [ ] The middle premolar in the upper and lower jaw is more reduced than in *M. mystacinus*. It is not clear which name applies to this form. It could be *Myotis przewalskii*." [our translation from German]. Recent research of the East Mediterranean populations of *M. mystacinus* was particularly contributed by the results of Volleth's (1987, 1989) karyological studies. She found two forms of the *M. mystacinus* group in Greece and Turkey, which were distinct from the Central European representatives of *M. mystacinus* and/or *M. brandtii*. Unlike Helversen (1989a, b), Volleth (1987, 1989) used for these populations only technical names, incl. *Myotis* sp. A and *Myotis* sp. B. Similar results were obtained from the molecular studies by Nemeth (1993) and Nemeth & Helversen (1993), respectively; they concluded: "there are at least three European species within the *M. mystacinus* group: *M. brandtii*, *M. mystacinus* (*mystacinus* and *przewalskii*) and *M.* spec." The latter two forms they found in Greece and Turkey, which makes it very probable that the studied specimens were of the same origin as those studies by Volleth (1987, 1989), Helversen (1989a, b), and Nemeth (1993). However, these results were not accepted by Koopman (1994), who listed from the whole western part of the Palearctic only the nominotypical subspecies *M. m. mystacinus*.

Tsytsulina (1999) studied in detail baculum, tooth and skull morphology, as well as cranial and external morphometry of *Myotis mystacinus* bats from the Caucasus region, distinguishing three different subspecies: *M. m. popovi*, a large form from the Caucasian and Ciscaucasian steppes; *M. m. aurascens* from all forested parts of the Caucasus Mts., Transcaucasia, and northern part of the Armenian Highlands; and *M. m. hajastanicus*, a relict form from the Sevan Lake basin in Armenia (2000 m a. s. l.), which does not occur in other parts of Transcaucasia.

M. mystacinus group is extremely variable in morphology (see also Benda & Horáček 1998). It can include temporarily divergent local populations, as well as clinal variation. Even parallel variation in distant lineages can be present here. In the middle of the 20th century, the single species started to be gradually splitted into several species, the number of which – not only in the western Palearctic – is unknown yet. At present, the occurrence of two species (*M. mystacinus* and *M. brandtii*) is well confirmed, but some data indicate that this number is not final, see e. g. Stubbe & Chotolchu (1968), Volleth (1987), Nemeth & Helversen (1993). This problem required a detailed revision of the species complex using a combined application of both the traditional and new taxonomic approaches.

We revised the systematics of *M. mystacinus* group using traditional methods of morphological comparison. In the present study, we evaluated all populations of the western part of the Palearctic, incl. those from the Mediterranean and the Caucasus regions.

MATERIAL AND METHODS

For the taxonomic analysis, museum specimens were used, belonging to the following nominal species. *Myotis brandtii*, *M. mystacinus* s. l. and *M. ikonnikovi* (together over 650 specimens from 17 museum collections, incl. most types). These three names (sensu Strelkov & Buntova 1982, Strelkov 1983a, b, Koopman 1993, 1994, etc.) are used for the respective samples and populations throughout the present paper (exceptions are specified below). A comprehensive list of all studied specimens, with data on their geographical origin and present deposition, is given in App. II (where the revised classification is used for lucidity). With exception of 29 specimens of *M. ikonnikovi* from Baikal region, East Siberia and the Far East, and type specimens of *M. mystacinus* s. l. from Asia, we examined only specimens of the *Myotis mystacinus* group from the western Palearctic, which we separated in population samples (see Figs. 1, 2). Juvenile and subadult individuals were not considered in this analysis (see Horaček 1979). Considering the results of previous investigations (Bogdanowicz 1992, Benda & Horáček 1995, etc.) the possible effects of sexual dimorphism were neglected in this study.

The specimens were measured with mechanical or optical calipers in the standard way. The height of the mesiopalatal cingular cusp of P^4 was measured according to Baagøe (1973: 197, Fig. 2). The terminology of molar characters follows Menu (1987). Bacula were extracted in 6% solution of KOH and coloured with alizarin red. The microphotographs of teeth were made by the scanning electron microscope BS 300 Tesla (courtesy of Dr. Ivo Klepáček, Institute of Anatomy, 1st Medical Faculty, Charles University, Praha).

For lucidity, the following two geographic terms are used in this paper. Middle Asia (= the former Soviet central Asian countries, older synonym Western Turkestan) and Central Asia (= Tibet, Chinese Turkestan [Sintiang = Xinjiang], and Mongolia, older synonym Eastern Turkestan s. l.)

NOMENCLATURAL NOTE. Haensel (2000) and Kock (2000) followed Woodman (1993) and the newest edition of the International Code of Zoological Nomenclature (ICZN 1999), and understand the genus name *Myotis* as a femininum. Hence, endings of species names should be corrected accordingly, which applies here to *Myotis mystacina*, *M coluota*, etc However, we continue to understand here *Myotis* as a masculinum, because it has been used so since 170 years, and hence was conserved in this way.

ABBREVIATIONS

COLLECTIONS BMNH – Natural History Museum, London, United Kingdom, BZM – Zoological Museum, Humboldt University, Berlin, Germany; EBD – Biological Station Doñana, Spain; MNHG – Natural History Museum, Genève, Switzerland; MTD – Zoological Museum Dresden, Germany, NMP – National Museum, Prague, Czech Republic; OHC – Otto von Helversen Collection, Erlangen, Germany (material was studied by Ivan Horáček, Prague, who kindly provided us with the data), PMS – Slovenian Natural History Museum, Ljubljana, Slovenia, NMW – Natural History Museum, Vienna, Austria, RMS – Royal Museum Stockholm, Sweden, SMF – Senckenberg Museum, Frankfurt am Main, Germany; TAU – Tel Aviv University, Israel; ZIN – Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia; ZMMU – Zoological Museum of the Moscow State University, Moscow, Russia; ZMS – Zoological Museum, Sofia, Bulgaria; ZMSO – Zoological Museum, Siberian Branch of Russian Academy of Science, Novosibirsk, Russia; ZZZ – Zoological Institute of Zagreb, Croatia.

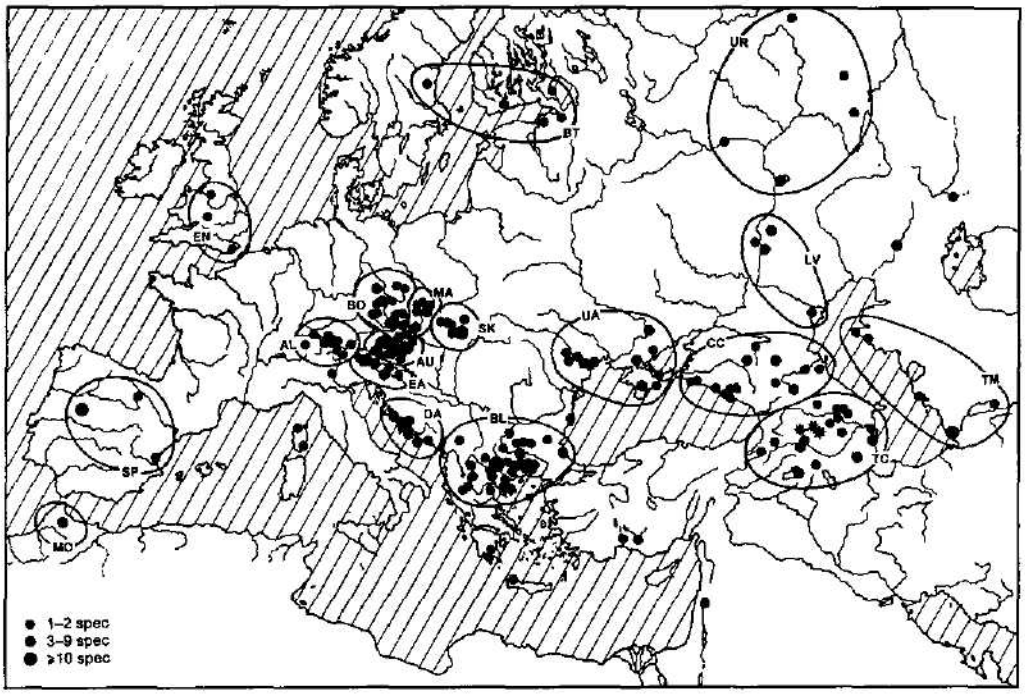


Fig 1 Map of the western Palearctic, showing localities of studied specimens of *Myotis mystacinus* s. l and geographic delimitation of population samples For abbreviations see p. 336; sample of Sevan Lake basin is marked by asterisks

Taxa (lower case letters). bra = *M. brandtii*, iko = *M. ikonnikovi*, mys = *M. mystacinus* s. l.

Geographical groups (upper case letters). These abbreviations are used in maps (Figs 1, 2), figures, and in the appendices II–III. **Simple samples** (in geographical order, from the west to the east, see Figs 1, 2): MO = Morocco, SP = Spain, EN = England, AL = central Alps (Switzerland, Vorarlberg, and West Tirol), AU = Austria (in *M. mystacinus* s. l. only the Upper and Lower Austria, Burgenland, and Styria, in *M. brandtii* whole Austria), BO = Bohemia, MA = Moravia (Moravia and the Czech part of Silesia), SK = Slovakia, EA = south-eastern Alps (Carinthia, East Tyrol, and Slovenia), DA = Dalmatia (incl. sea islands), BL = northern Balkans (Montenegro, Kosovo, Macedonia, Bulgaria, and northern Greece), UA = Ukraine (southern Ukraine, incl. Crimea and Moldavia), CC = Ciscaucasia and North Caucasus Mts. (i. e., Russian part of Caucasus region), TC = Transcaucasia and the Great Armenia (Transcaucasian countries, NE Turkey and NW Iran), SB = Sevan Lake basin in Armenia. LV = Lower Volga region, BT = northern Baltic (Finland, Sweden, Estonia, and St. Petersburg region of Russia), RU = Central and Eastern parts of European Russia, UR = Ural Mts. region, TM = western Turkestan (W Turkmenistan and SW Kazakhstan), ET = eastern Turkestan (type series of *Myotis mystacinus przewalskii* Bobrinskoj, 1926). **Aggregate samples** (in alphabetical order): CE = Central Europe (material from AL, AU, BO, MA, SK and EA), CZ = Czech Republic (material from BO and MA), CA = Caucasus region (material from CC and TC), N = northern samples (material from CE and NE), NE = northeastern Europe (material from BT, RU and UR), S = southern samples (material from DA, UA, and LV).

Measurements. **Cranial and dental measurements**: LCr = greatest length of skull, LCb = condylobasal length of skull, LaZ = zygomatic width, LaI = width of interorbital constriction, **LaInf** = width between foramina infraorbitalia, LaN = neurocranium width, ANc = neurocranium height, ACr = skull height (incl. bullae tympanicae), CC = rostral width between canines (incl.), P^4P^4 = rostral width between third upper premolars (incl.), M^3M^3 = rostral width between third upper molars (incl.), IM^3 = length of upper teeth-row between IM^3 (incl.), CM^3 = length of upper teeth-row between CM^3 (incl.), P^4M^3 = length of upper teeth-row between P^4M^3 (incl.), M^1M^3 = length of upper teeth-row between M^1M^3 (incl.), M^1M^2 = length of upper teeth-row between M^1M^2 (incl.), CP^4 =

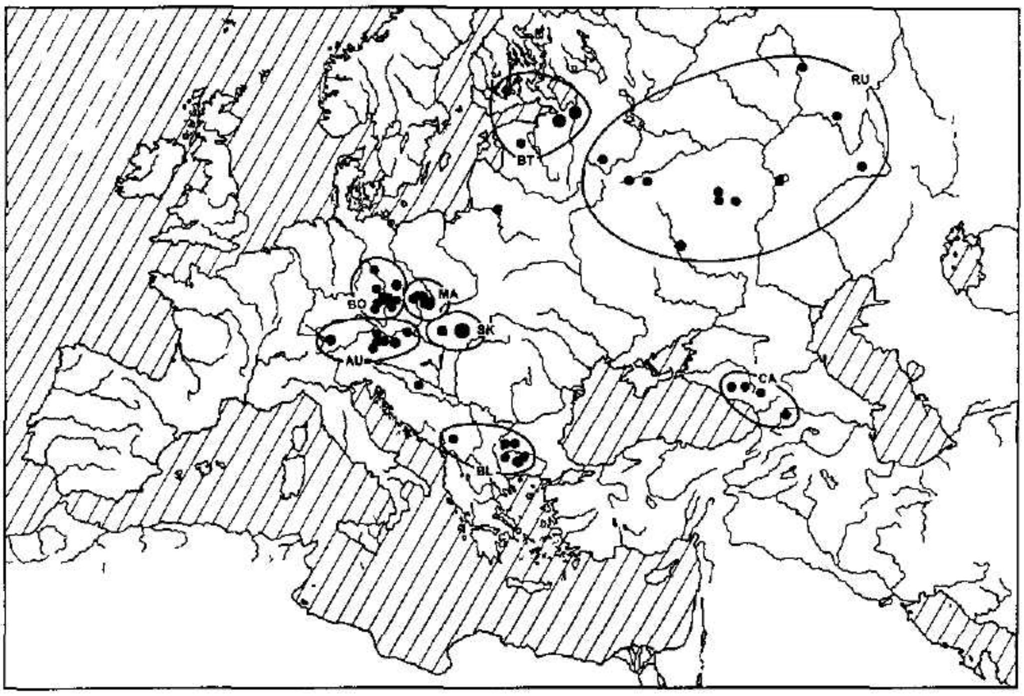


Fig. 2. Map of the western Palearctic, showing localities of studied specimens of *Myotis brandtii* and geographic delimitation of basic populations. For abbreviations see p. 336.

length of upper teeth-row between CP^4 (incl.), P^2P^3 = length of upper teeth-row of P^2 and P^3, LP^3 = mesiodistal length of second upper premolar, LMd = mandible length, ACo = height of coronoid process, IM_3 = length of lower teeth-row between IM_3 (incl.), CM_3 = length of lower teeth-row between CM_3 (incl.); P_4M_3 = length of lower teeth-row between P_4M_3 (incl.); M_1M_3 = length of lower teeth-row between M_1M_3 (incl.); CP_4 = length of lower teeth-row between CP_4 (incl.), P_2P_3 = length of lower teeth-row of P_2 and P_3; LP_3 = mesiodistal length of second lower premolar, LaP^4 = palatolabial width of third upper premolar; LaM^1 = palatolabial width of first upper molar, LaM^2 = palatolabial width of second upper molar; LaM^3 = palatolabial width of third upper molar, ACin = height of mesiopalatal cingular cusp of P^4, LCn = mesiodistal length of upper canine; LaCn = palatolabial width of upper canine, RCn = relative width of upper canine (LCn · LaCn ratio). **Wing measurements** LAt = forearm length; LPol = thumb length; LMcV = Vth metacarp length; LMcIV = IVth metacarp length, LMcIII = IIIrd metacarp length, LMcII = IInd metacarp length; LPVp = length of Vth proximal phalanx, LPVm = length of Vth medial phalanx; LPIVp = length of IVth proximal phalanx; LPIVm = length of IVth medial phalanx, LPIIIp = length of IIIth proximal phalanx, LPIIIm = length of IIIrd medial phalanx; LTib = length of tibia

RESULTS

Dimensional characters

SKULL. Skull size is highly variable within the group. Figs 3–5 show the skull variability using three longitudinal dimensions (greatest length of the skull, mandible length, and length of the upper teeth-row, CM^3). It was shown, that (1) *M. ikonnikovi* has the smallest skull; (2) the inter-sample variability in *M. brandtii* is rather low, but northern specimens (from Central and north-eastern Europe) tend to be larger, while southern specimens (from AU, BL, and CA) smaller; (3) skull size is most variable in *M. mystacinus* s. l. In the latter species, three types of size can be observed, as follows: (a) small-sized individuals from "northern" countries (EN; AL, AU, BO, MA, SK, EA; BT, UR; i. e. England, Central and north-eastern Europe) and western Turkestan (TM), (b) large-sized individuals from the Mediterranean and south-eastern Europe (MO, SP, DA, UA, LV) and eastern Turkestan (ET), and (c) highly variable samples, which cannot be assigned to any of the former two categories, incl. the Balkans (BL) and the Caucasus region (CC, TC, SB). Particular data are given in App. III.

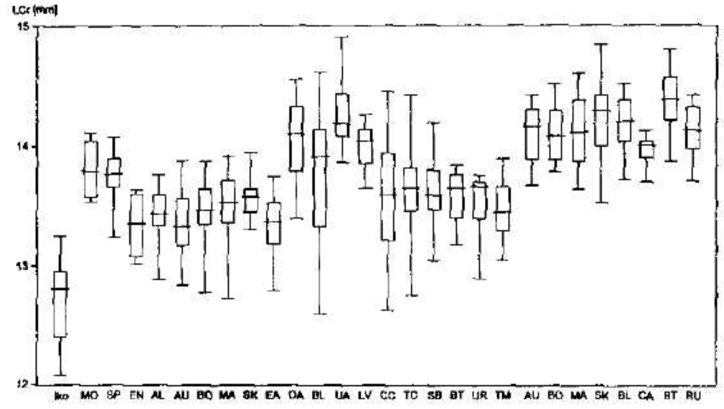
TEETH. Similar sample groups as in the case of skull dimensions were found on the basis of dental measurements (see App. III). Some of the data are presented in Figs 6–11.

Fig. 6 shows the variability in molars length on the example of the M^1M^2 row. *M. brandtii* and *M. mystacinus* s. l. are similar to each other in this dimension, but *M. brandtii* has a larger skull, so that the upper teeth-row is relatively shorter in this species. Length of M^1M^2 is rather uniform in all samples of *M. mystacinus* s. l., but it is shorter in north-eastern samples (BT, UR), where it reaches values of *M. ikonnikovi*. On the other hand, "southern" samples (SP, DA, UA) and the sample from eastern Turkestan (ET) have longest M^1M^2. The Balkan sample (BL) is most variable in this respect.

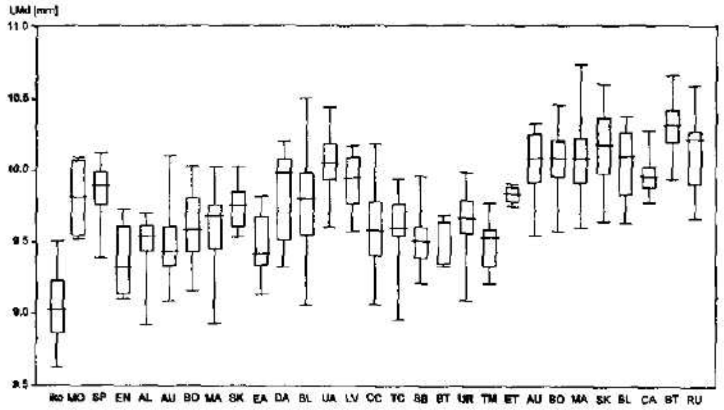
A comparison of premolar-rows (P^2P^3 and P_2P_3) resulted in a different observation (see Fig. 7). In this respect, most of samples of *M. mystacinus* s. l. are similar to *M. brandtii*, and also to *M. ikonnikovi*. Samples of *M. mystacinus* s. l. from eastern populations, i. e. those from Turkestan (TM, ET), are quite different, premolar-rows are more shorter. The Balkan sample (BL) is most variable also in these characters.

Height of the mesiopalatal cingular cusp of P^4 (Fig. 8) is a traditional taxonomical character in the *M. mystacinus* group. Its comparison resulted in similar observations as the analysis of skull dimensions (see above). Again, a group of samples corresponding to the species *M. brandtii* was separated (cusp height = 0.11–0.34 mm). In the remaining samples (*M. mystacinus* s. l. and *M. ikonnikovi*), three groups could be distinguished, which corresponded with geographical groups defined above: (1) *M. mystacinus* s. l. with a rather high cingular cusp of P^4 (0.04–0.21 mm), with "northern" samples (Central and north-eastern Europe), and also west Mediterranean samples and *M. ikonnikovi*; (2) *M. mystacinus* s. l. with a low or absent mesipalatal cingular cusp of P^4 (0–0.11 mm), with

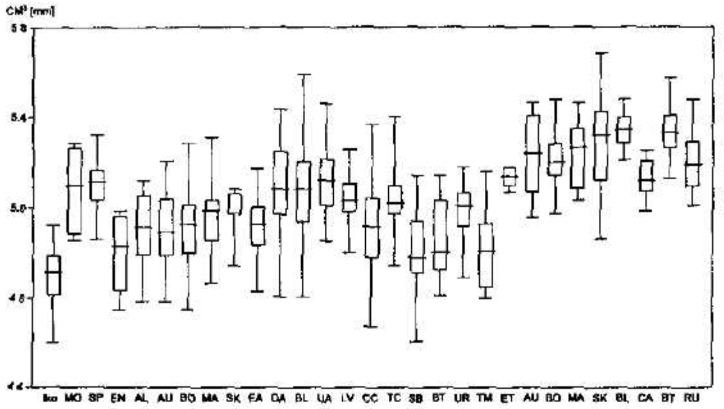
3



4

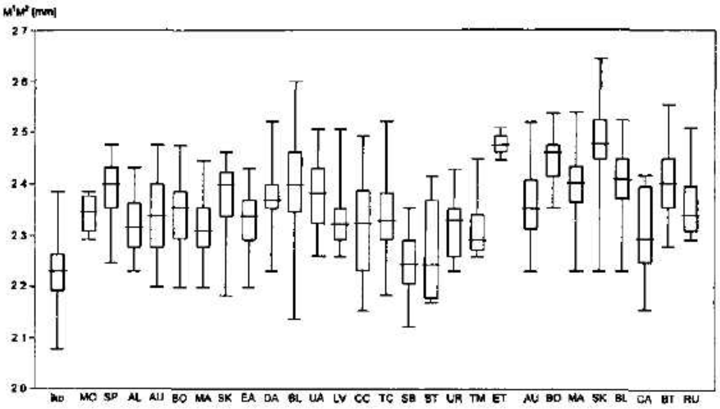


5

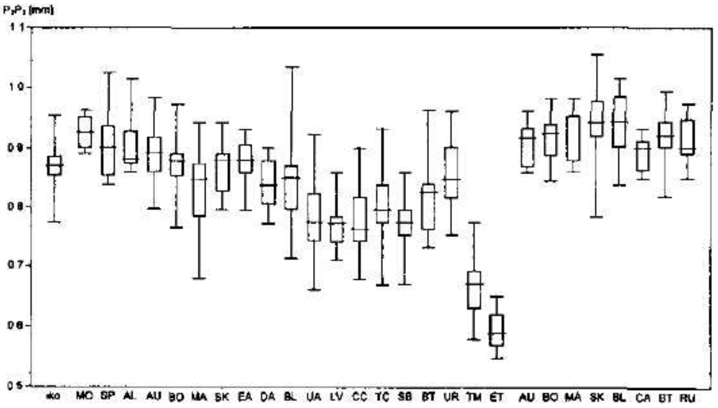


Figs 3–5. Variation in three skull measurements in the examined samples of the *Myotis mystacinus* group. Thin line – *M. mystacinus* s. l., thick line – *M. ikonnikovi* (iko, first left box) and *M. brandtii* (right boxes). For abbreviations see p. 336. 3 – greatest length of skull (LCr). 4 – mandible length (LMd). 5 – length of upper teeth-row (CM^3).

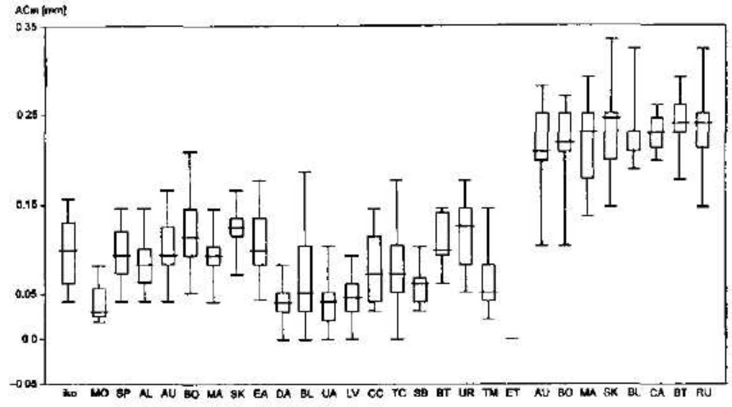
6



7

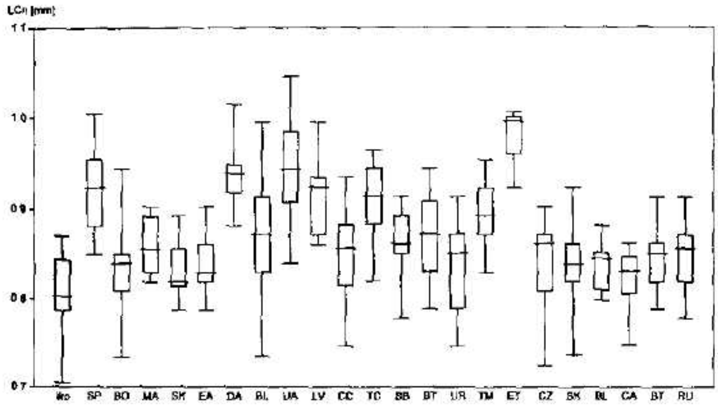


8

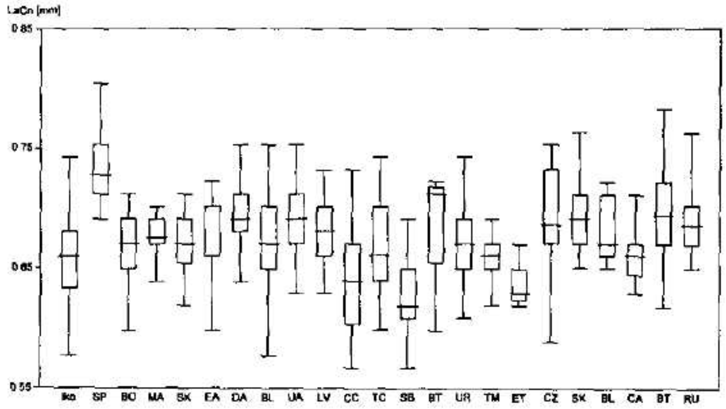


Figs 6–8. Variation in three teeth-row measurements in the examined samples of *Myotis mystacinus* group. Thin line – *M. mystacinus* s. l., thick line – *M. ikonnikovi* (iko, first left box) and *M. brandtii* (right boxes). For abbreviations see p. 336. 6 – length of upper molar-row (M^1M^2). 7 – length of lower premolar-row (P_2P_3). 8 – heigth of the mesiopalatal cingular cusp of P^4 (ACin).

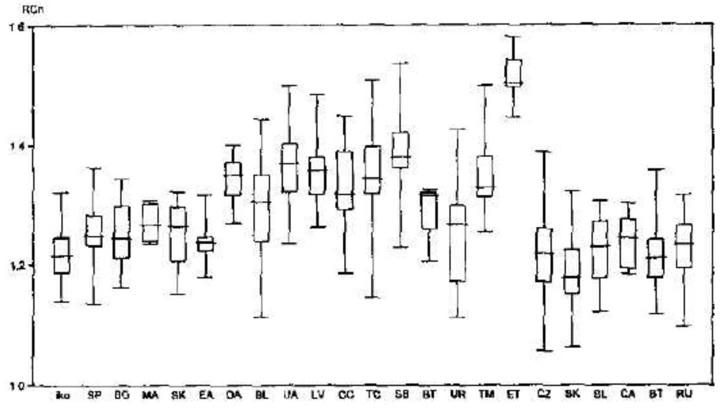
9



10



11



Figs 9–11. Variation in three dimensions of the upper canine in the examined samples of *Myotis mystacinus* group. Thin line – *M. mystacinus* s. l., thick line – *M. ikonnikovi* (iko, first left box) and *M. brandtii* (right boxes). For abbreviations see p. 336. 9 – length of upper canine (LCn). 10 – width of upper canine (LaCn). 11 – relative width of the upper canine (RCn = LCn / LaCn).

"southern" samples (DA, UA, LV), and also eastern samples (TM, ET), in which is higher cusp on average, however, and (3) group of samples from the Balkans and Caucasus (BL, CC, TC) with variable height of the cingular cusp of P^4 Samples from Morocco and Sevan Lake basin (MO, SB) are of uncertain position

A comparison of the relative and absolute length and width of the upper canine in *M mystacinus* group (Figs 9–11, 33) again allowed to discern three groups (see Fig 11) (1) group with rather rounded canine (low values of RCn), with *M ikonnikovi*, *M brandtii*, and "northern" and west Mediterranean (SP) samples of *M mystacinus* s l , (2) group with rather narrow canine, with "southern" (DA, UA, LV), "eastern" (TM, ET) and Sevan Lake basin (SB) samples of *M mystacinus* s l , and (3) highly variable samples, in which both types of canines occur, i e those from the Balkans and from Caucasus (BL, CC, TC) As shown in Fig 10, the canine width is almost the same in all samples, excepting the west Mediterranean sample (SP), in which the canine is rather round, so that we included it in the category (1), but absolutely most broad, forming thus a special group within the latter category

WING Parameters describing the wing size are rather variable within samples (see App III) Figs 12–14 show the variability of the forearm length (LAt), length of the Vth metacarpus (LMcV), and length of the proximal phalanx of the Vth finger (LPVp) It results from this comparison, that no substantial differences exist between nominal species Most variable are again samples from the Balkans (BL) and from Caucasus region (TC) Largest wings have bats from Sevan Lake basin (SB), smallest wings those of *M ikonnikovi* (iko) samples

Dental characters

MOLARS Size of the three upper molars (M^1, M^2, M^3) is not equally variable (see App III) Width of M^3 (character LaM^3) is roughly same in all compared samples, width of M^1 (character LaM^1) is rather variable, and width of M^2 (character LaM^2) is intermediate in this respect M^1 is widest in most samples of *M brandtii* and in "southern" samples of *M mystacinus* s l (UA, DA, LV, CC), i e in bats with the largest skull M^1 is least wide in *M ikonnikovi* (i e in bats with the smallest skull), and in *M mystacinus* s l from Sevan Lake basin (SB) Width of M^1 is thus positively correlated with the skull size in the whole group, but in the latter sample

Also the presence/absence and size of cusps and crests on the occlusion surface of molars is rather variable, incl presence/absence of paraconules, paralophs, metaconules and metalophs on M^1 and M^2, and on the presence/absence of paraconules and paralophs on M^3, respectively (see Tab 1) All four features are well developed in *M brandtii*, where they are absent only in a minority of cases, while their presence/absence is variable in the remaining groups Only the presence of the paraconule and metaloph is thus of some interest these characters are mostly absent in *M mystacinus* s l and *M ikonnikovi* It is possible to summarize, that characters on the occlusion surface of molars are of minor importance for the identification of bats of the studied group, with the exception of *M brandtii*

PREMOLARS Metrical differences in the length of the premolar-row, and in the heigth of the cingular cusp of P^4 were discussed in the previous chapter. Another character, which is variable within the group under study, is the size and position of P^3 in relation to the axis of the teeth-row P^{2}P^4 Three states of this character can be distinguished (see Tab 1) (1) cusp of P^3 is located on the axis between the cusps of P^2 a P^4, and is rather large (ca $^1/_3$ to $^2/_3$ of the size of P^2), (2) cusp of P^3 is located approximately on the axis between the cusps of P^2 a P^4, but is rather small (ca $^1/_4$ to $^1/_2$ of the size of P^2), and (3) P^3 is rather small, and located palatally from the teeth-row States (1) and (2) are rather common, while the situation (3) is very rare, being most often found in the "southern" and "eastern" samples of *M mystacinus* s l (UA, LV, TC, TM) The state (3) occurs only exceptionally, or not at all in other samples

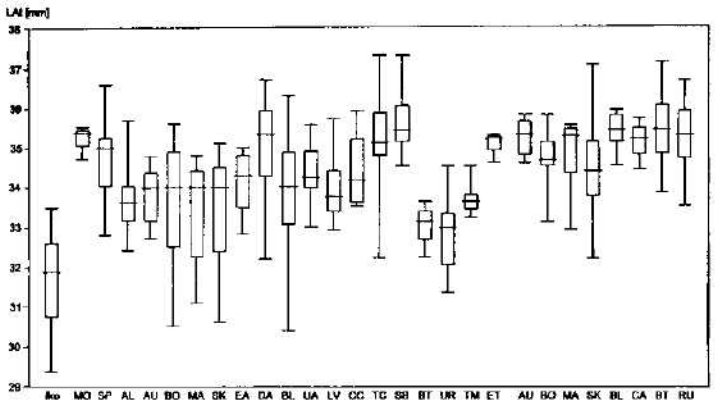
Tab 1 Proportion per cent of dental phenotypes in the studied samples of the *Myotis mystacinus* group Explanation of phenotypic categories position of P^3. 1 – cusp of P^3 lays approximately in the axis of the cusps of P^2 and P^4, 2 – cusp of P^3 lays palatally off the axis, 3 – P^3 lays palatally, outside the premolar-row; characters on M^1 and M^2 0 – character absent, 1 – character slightly developed, 2 – character well developed Values higher than 50% are printed in **bold** in the case of molar characters

character	P^3-position			paraconule		paraloph			metaconule			metaloph		
phenotype	1	2	3	0	2	0	1	2	0	1	2	0	1	2
M. mystacinus s. l.														
MO	100	–	–	**100**	–	–	–	**100**	–	**100**	–	–	–	**100**
SP	100	–	–	**92**	8	31	50	19	38	38	24	**56**	25	19
EN	75	25	–	**100**	–	50	25	25	**100**	–	–	**75**	25	–
AL	86	14	–	**100**	–	40	50	10	24	38	38	**52**	29	19
AU	85	15	–	**100**	–	25	**56**	19	6	49	45	37	46	17
BO	100	–	–	**100**	–	**68**	26	6	35	**54**	11	**91**	9	–
MA	93	7	–	**95**	5	**60**	12	28	29	38	33	**89**	4	7
SK	93	7	–	**100**	–	50	43	7	**72**	14	14	**93**	7	–
EA	80	5	5	**100**	–	33	**52**	15	35	47	18	**64**	23	13
DA	86	9	5	**86**	14	27	**59**	14	36	19	45	**55**	36	9
BL	85	11	4	**96**	4	31	45	24	41	32	27	**66**	21	13
UA	76	21	3	**88**	12	12	**62**	26	15	34	**51**	47	44	9
LV	76	12	12	**81**	19	13	31	**56**	–	19	**81**	**63**	31	6
CC	80	8	12	**100**	–	**46**	29	25	29	46	25	**68**	24	8
SB	100	–	–	**94**	6	47	47	6	18	35	47	24	41	35
TC	76	12	12	**100**	–	35	50	15	29	**53**	18	**56**	32	12
BT	67	33	–	**100**	–	33	50	17	33	33	33	50	50	–
UR	100	–	–	**93**	7	21	36	43	7	50	43	**57**	43	–
TM	58	25	17	**64**	36	27	20	**53**	20	7	**73**	**60**	27	13
ET	75	25	–			**100**	–	–	50	–	50	**100**	–	–
mysCE	90	9	1	**99**	1	45	40	15	29	43	28	**69**	21	10
mysNE	90	10	–	**95**	5	25	40	35	15	45	40	**55**	45	–
mysS	79	15	6	**86**	14	17	**54**	29	18	26	**56**	**52**	39	9
M. brandtii														
AU	81	19	–	23	**77**	–	13	**87**	–	20	**80**	13	31	**56**
BO	100	–	–	18	**82**	–	16	**94**	–	33	**67**	6	17	**77**
MA	93	7	–	42	**58**	–	23	**77**	9	33	**58**	13	13	**74**
SK	100	–	–	23	**77**	4	7	**89**	–	29	**71**	3	10	**87**
BL	100	–	–	29	**71**	11	–	**89**	–	33	**67**	–	–	**100**
CA	100	–	–	20	**80**	–	17	**83**	–	29	**71**	–	14	**86**
BT	100	–	–	36	**64**	–	15	**85**	–	40	**60**	15	35	**50**
RU	100	–	–	31	**69**	–	29	**71**	7	36	**57**	–	24	**76**
braCE	95	5	–	25	**75**	1	11	**88**	2	29	**69**	8	16	**76**
M. ikonnikovi														
iko	100	–	–	**100**	–	34	38	28	22	**52**	26	48	35	17

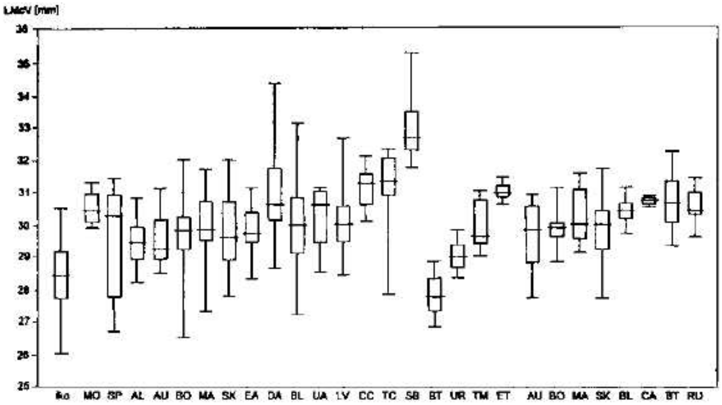
Length of the smallest premolars P^3 and P_3 (characters LP^3 and LP_3) is correlated with the size and position of P^3 (see App. III.). Both these teeth are smallest in eastern samples of *M. mystacinus* s. l. (TM, ET), very small are also in southern samples of *M. mystacinus* s. l. (DA, UA, LV, SB). On the other hand, both the teeth are largest in "northern" and west Mediterranean samples of *M. mystacinus* s. l., and in *M. brandtii* and *M. ikonnikovi*. It can be concluded, that length of P^3 and its position are correlated: the smaller is P^3, the more it tends to displace palatally, and vice versa.

Variations in the height of the cingular cusp of P^4 was described in the previous chapter. However, the latter character is probably not correlated with the width of P^4, which is largest in *M. brandtii*,

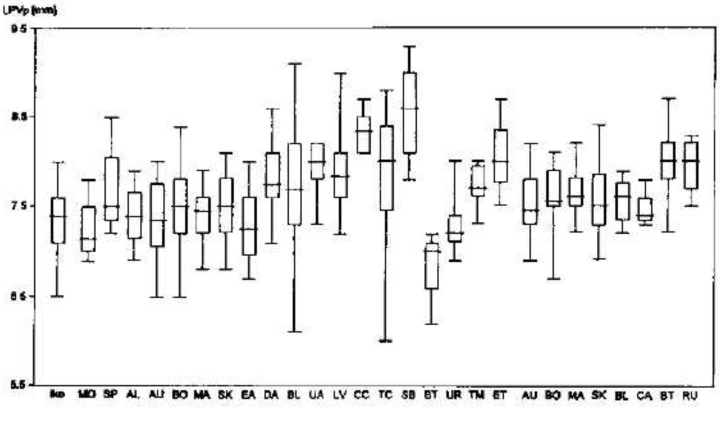
12



13



14



Figs 12–14. Variation in three wing measurements in the examined samples of *Myotis mystacinus* group. Thin line – *M. mystacinus* s. l., thick line – *M. ikonnikovi* (iko, first left box) and *M. brandtii* (right boxes). For abbreviations see p. 336. 12 – forearm length (LAt). 13 – length of the fifth metacarp (LMcV). 14 – length of the fifth proximal phalanx (LPVp).

where the cusp of the cingulum on P^4 is highest, and – at the same time – in southern samples of *M. mystacinus* s. l. (MO, SP, UA, LV), where the cingular cusp of P^4 is smallest (or just absent). P^4 is least wide in *M. ikonnikovi*, being medium wide in the remaining samples of *M. mystacinus* s. l. This means, that width of P^4 is correlated with the skull size (similarly as width of molars, see above), not with the size of the cingular cusp.

CANINES. As mentioned above, samples significantly differ in the size of the cingulum of the upper canine. The length to width relation of the upper canine (RCn) allowed to discern two basic groups of studied bats: (1) samples with long and narrow canine, and (2) samples with short and rounded canine. In addition, both types of canines occur in some samples (BL, CC, TC of *M. mystacinus* s. l.).

The shape of the type (1) of canines is formed not only by the rather rounded cingulum (in occlusion view), as indicated by the low value of length/width ratio, but also broad and pseudotriangular basis of the canine crown (see Figs 53–56). This canine is rather robust, with distinct distopalatal basal concavity; distolabial basal concavity is less distinct, and on the anterior surface is sometimes developed only a groove. As mentioned above, this type of canines is found in *M. brandtii*, *M. ikonnikovi*, in "northern" samples of *M. mystacinus* s. l. (Central and north-eastern Europe), and in west Mediterranean samples. However, canines are very large and robust in the latter sample (SP), although their relative width is approximately the same as in other samples from the group (1).

Narrowed shape of the upper canine of the type (2) is formed by the rather rhombic shape of cingulum and the basis of canine crown. The canine has a rather slender point with four more or less well developed mesial, distal, palatal and labial edges. These edges enclose grooves or convexities, of which the distopalatal and distolabial are best developed, while the grooves between both lateral edges and the mesial edge are less distinct, although mesiopalatal groove is almost always present. This type of canines was found only in a few samples of *M. mystacinus* s. l., particularly in DA, UA, LV, SB, TM, ET, and in some individuals from BL, CC and TC. Bats from the Sevan Lake basin (SB) have a "narrow" canine, with the above mentioned characters, but it is very short, with which the slenderness is correlated (see Figs 42, 58).

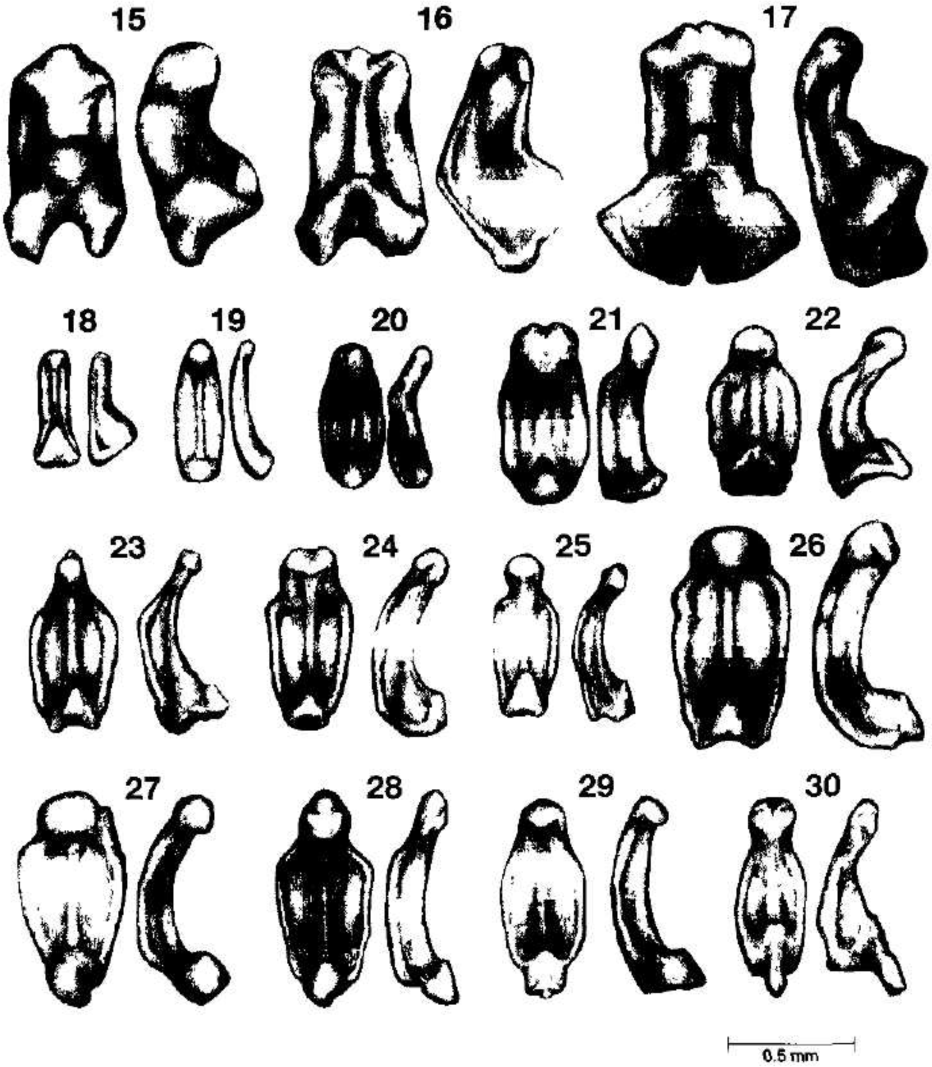
INCISIVES. The second upper incisive (I^2) has a variable presence of a cusp on the "palatal" edge of cingulum. The latter cusp is most often, and in a most distinct way developed in north-eastern samples of *M. mystacinus* s. l. (BT, UR), but was also found in samples of *M. mystacinus* s. l. from Central Europe and from the Balkans. The cusp is developed at most as a small protuberance in *M. brandtii* and *M. ikonnikovi*, while it is developed only as an incision on the palatal edge of the cingulum of I^2 in "southern" and "eastern" samples of *M. mystacinus* s. l. (see Figs 67–72).

Baculum characters

Bacula fall in three basic types (see Figs 15–30), which correspond to the three recognized nominal species of the material under study. First type belongs to *M. brandtii* (Figs 15–17) from all parts of its geographic range. It is a robust bone with broadened distal epiphysis ("head"), very broad and bifurcated proximal epiphysis, and broadened diaphysis, ventrally concave. Baculum of this type has only small lateral "wings", the bone has a shape of a pyramid. The length of baculum is 0.80–1.07 mm, proximal width 0.51–0.83 mm. The smallest baculum (length 0.8 mm only) of *M. brandtii* was recorded in the Caucasus sample (CA) of the species.

Second type includes the bacula of *M. ikonnikovi* (Fig. 18). This baculum is smallest, reaching maximally 0.5 mm in length. Distal epiphysis is narrow, and no "head" is formed. Proximal epiphysis has a shape of a broad triangle in lateral view. The diaphysis lacks "wings". The whole bone is narrow and straight in dorsal view.

The last, highly diversified type is formed from the bacula of *M. mystacinus* s. l. (Figs 19–30). They are oval in shape (in dorsal view), concave from the ventral side, have a narrow diaphysis, and



Figs 15–30. Examples of baculum preparates of examined populations of *Myotis mystacinus* group. Left – dorsal aspect, right – lateral aspect (dorsum to the right). 15 – *M. brandtii*, ZIN 55710, Staraja Ladoga (Volhov Dist.), Leningrad Reg., Russia; 16 – *M. brandtii*, ZIN 9020, S-Ural Mts., Orenburg Reg., Russia; 17 – *M. brandtii*, NMP 48482, Ladenica cave (Smoljan Dist.), Bulgaria; 18 – *M. ikonnikovi*, NMP 48543, Svjatoj Nos isthmus, Burjatskaja Rep., Russia; 19 – *M. mystacinus* s. s., NMP 48344, Gorna Breznica (Blagoevgrad Dist.), Bulgaria; 20 – *M. mystacinus* s. s., ZIN 37913, Div'ja cave (Nyrob Dist.), Perm Reg., Russia; 21 – *M. mystacinus* s. s., ZIN 8998, Terter river, Azerbaijan; 22 – *M. mystacinus* s. s., NMP 47915, Van (Van Dist.), Turkey; 23 – *M. nipalensis*, ZIN 5104, Xiao Qaidam Hu Lake (Qaidam Pendi Basin, E-Tibet), China; 24 – *M. aurascens*, ZIN 62425, Meleşti (Chişinau Dist.), Moldavia; 25 – *M. aurascens*, ZIN 68508, Mt. Karadag, Crimea Reg., Ukraine; 26 – *M. aurascens*, ZIN 70419, Berežnovka, Volgograd Reg., Russia; 27 – *M. aurascens*, ZMS No. 92, Beli Iskar dam (Sofija Dist.), Bulgaria; 28 – *M. aurascens*, ZIN 65239, Emba river, Aktjubinsk Reg., Kazakhstan; 29 – *M. aurascens*, NMP 48094, Sirbasan (Kars Dist.), Turkey; 30 – *M. aurascens*, NMP 48345, Stavros, Crete, Greece.

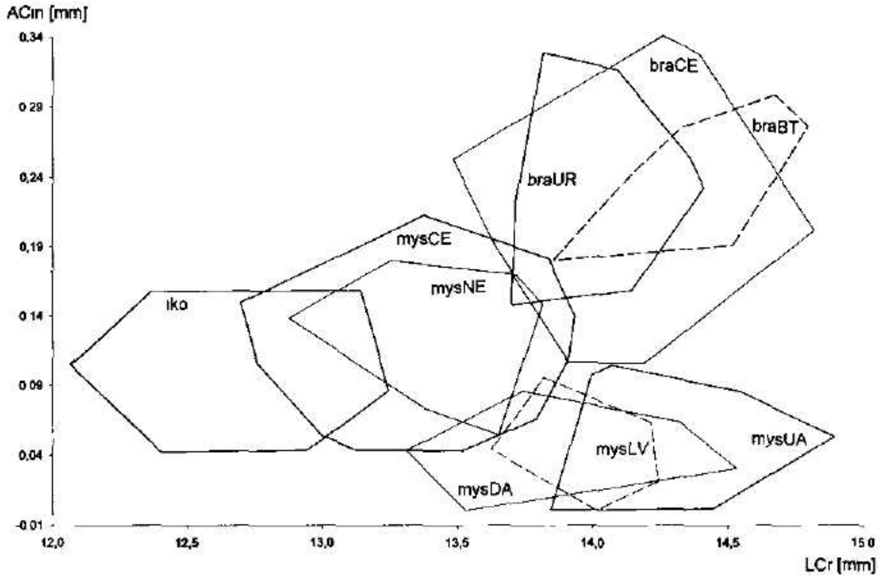


Fig. 31. A comparison of the greatest length of skull (LCr) versus height of mesiopalatal cingular cusp of P^4 (ACin), only samples with "low" variation were included. For abbreviations see p 336

more or less broad "wings". Thickened parts could be observed on both epiphyses. The baculum of this type is 0.57–0.92 mm long, reaching the maximum width (in its medial part) of 0.5 mm. Several subgroups can be distinguished within this group: (1) small knob-like baculum, ca. 0.6 mm long, with middle-narrow dorsal keel and rather narrow "heads" on both epiphyses (Figs 19, 20). In lateral view, this is a flat baculum with less diversified epiphyses. This type of baculum was found in bats from the Central and north-eastern Europe and from the Balkans. (2) Middle-sized baculum (length ca. 0.7 mm, width ca. 0.4 mm) with a broad proximal epiphysis and rather narrow distal epiphysis, broad keel on the dorsal side of the epiphysis, and rather narrow "wings" with robust edges (Figs 21, 22). In lateral view, a dorsal protuberance is visible on the proximal epiphysis. This type of baculum was found in bats from the Caucasus region. (3) Middle-sized to large baculum (length 0.67–0.92 mm, width 0.36–0.50 mm) with distinctly thickened parts on both epiphyses (Figs 23–30). The thickening is more distinct on the proximal epiphysis, where it is divided by a narrow groove in some cases. On the dorsal side of the diaphysis, very slender keel and broad "wings" with narrow thickened margins are present. This type of baculum was found in the bats from the Balkans, south-eastern Europe, the Caucasus region, and Turkestan. An exception is the specimen from Crete (Fig. 30), the baculum of which generally agrees with the bacula of the type (3), but which somewhat resembles the baculum of *M ikonnikovi* in the lateral view. This baculum has a flat and broad distal epiphysis, dorsoventrally thickened proximal epiphysis, and narrow "wings".

Bivariate comparisons

The results presented above indicate, that studied bat populations fall into two basic groups: (1) samples with low variability, and (2) highly variable samples. The first group includes all samples of

M. brandtii, *M. ikonnikovi*, samples of *M. mystacinus* s. l. from central and north-eastern Europe (AL, AU, BO, MA, SK, EL; BT, UR), some samples from southern and south-eastern Europe (MO, SP, DA, UA, LV) and from Middle Asia (SB, TM, ET). The latter group includes three samples from the Balkans (BL), Ciscaucasia (CC), and Great Armenia (TC) Before the analysis, some samples were lumped into larger samples (central Europe – CE, north-eastern Europe – NE). Size character described in the previous chapter were used here and are shown in Figs 31–34. Southern samples MO, SP, SB, and TM were excluded of this analysis for reasons mentioned above and are treated separately with the Mediterranean samples.

A plot of skull size (represented by the LCr dimension) against the height of cingular cusp on P^4 (Fig. 31) splitted the total sample into four clusters: (1) *M. brandtii* (large skull × high cusp), (2) *M. ikonnikovi* (small skull × midle-sized cusp), (3) "northern" samples of *M. mystacinus* s. l. (CE, NE; middle-sized skull × middle-sized cusp), and (4) southern samples of *M. mystacinus* s. l. (DA, UA, LV, large skull × low or absent cusp).

Bivariate comparison of molar- and premolar-rows (Fig. 32; specimens of *M. brandtii* were not included for lucidity) shows, that the "eastern" samples, i. e. those from the western and eastern Turkestan (TM, ET) are well different from the remaining samples. The length of the molar-row is closely correlated with the skull size, while the premolar-row is disproportionally shortened in "eastern" samples in comparison with all other samples. The premolar-row is the longest in the central European bats (CE). The sample from eastern Turkestan has the molar-row relatively long, while the premolar-row relatively short.

The relation between canine length (LCn) and relative width (RCn) allows to separate two groups of *M. mystacinus* (Fig. 33): (1) "southern" samples of *M. mystacinus* s. l. and the sample from eastern Turkestan (ET), which have long and narrow canines, and (2) remaining samples (*M*

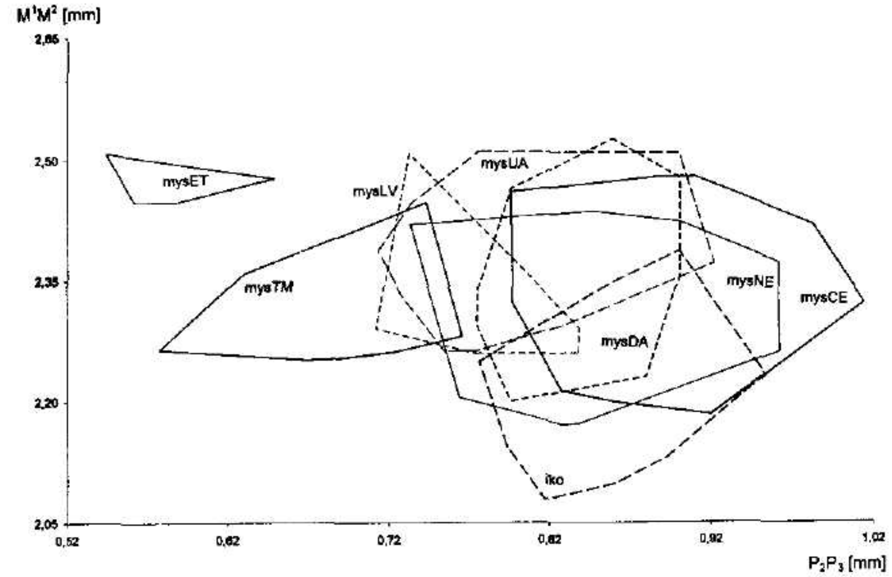


Fig. 32. A comparison of the length of lower premolar-row (P_2P_3) versus upper molar-row (M^1M^2), only samples with "low" variation were included. For abbreviations see p. 336.

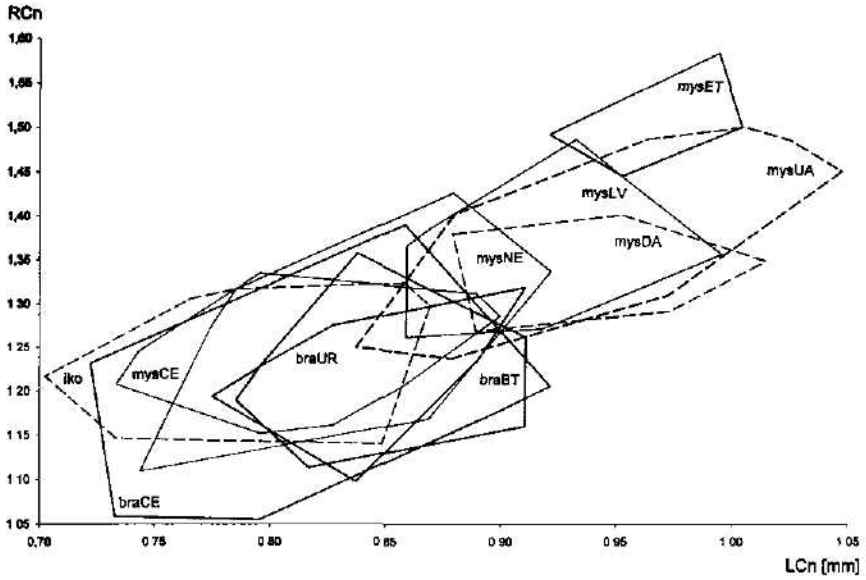


Fig 33 A comparison of the length (LCn) versus relative width (RCn) of upper canine, only samples with "low" variation were included For abbreviations see p 336

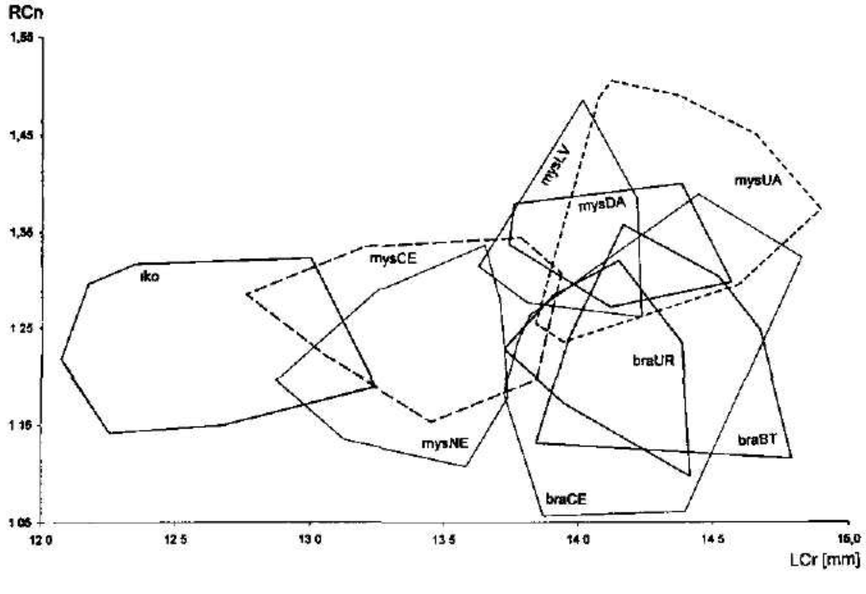


Fig 34 A comparison of the greatest length of skull (LCr) versus relative width of the upper canine (RCn), only samples with "low" variation were included For abbreviations see p 336

brandtii, *M. ikonnikovi*, and "northern" samples of *M. mystacinus* s. l.). When the relative width of the canine is compared with the skull size (Fig. 34), the same four groups of bats can be distinguished as shown in Fig. 31.

It follows from the above mentioned comparisons of cranial, dental and penial characters (both metrical and morphological), that five groups can be distinguished in the studied material. The groups overlap, but can be well defined and all include many specimens. It is the following five groups: *M. brandtii*, *M. ikonnikovi*, "northern" samples (CE, NE), "southern" samples (DA, UA, LV), and "eastern" samples (TM, ET) of the nominate *M. mystacinus* s. l.

M. mystacinus group in the Mediterranean and Caucasus regions

As evidenced in previous chapters, the range of metrical characters of Mediterranean samples (s. l., incl. those from the Caucasus region) is larger than in the remaining studied samples. Hence, samples from the both types of populations are compared in the following text.

Balkan population

The Balkan sample is highly variable in most of the studied metrical and morphological characters (see Figs 35 and 36). The observed pattern of variation suggests that the Balkan sample includes specimens from all three European "low-variation" units, incl. *M. brandtii*, "southern" populations of *M. mystacinus* s. l. and "northern" populations of *M. mystacinus* s. l., while *M. ikonnikovi* is different in skull size. Balkan specimens previously identified as *M. brandtii* fall in the polygon of *M. brandtii* from northern populations, while specimens identified as *M. mystacinus* s. l. fall into two polygons, which correspond with the "northern" and "southern" populations. This means,

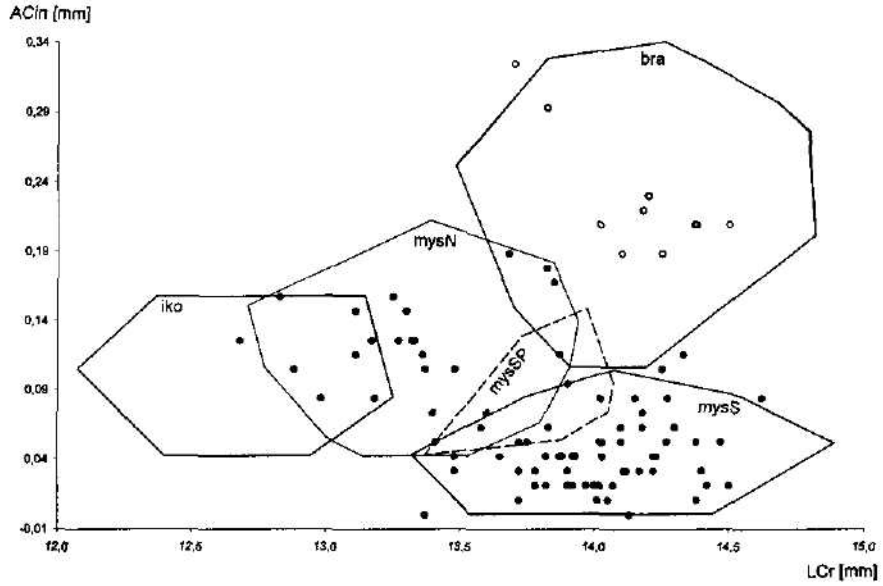


Fig. 35. A comparison of the greatest length of skull (LCr) versus height of mesiopalatal cingular cusp of P^4 (ACin). Polygons – samples with low variation, symbols – Balkan population (dots – *Myotis mystacinus* s. l., circles – *M. brandtii*). For abbreviations see p. 336.

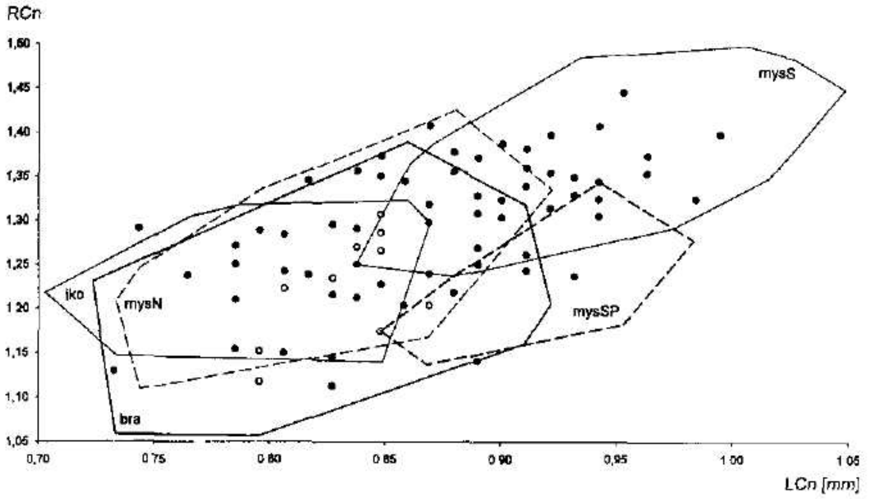


Fig 36 A comparison of length (LCn) versus relative width (RCn) of the upper canine Polygons – samples with low variation, symbols – Balkan population (dots – *Myotis mystacinus* s l., circles – *M brandtii*) For abbreviations see p 336

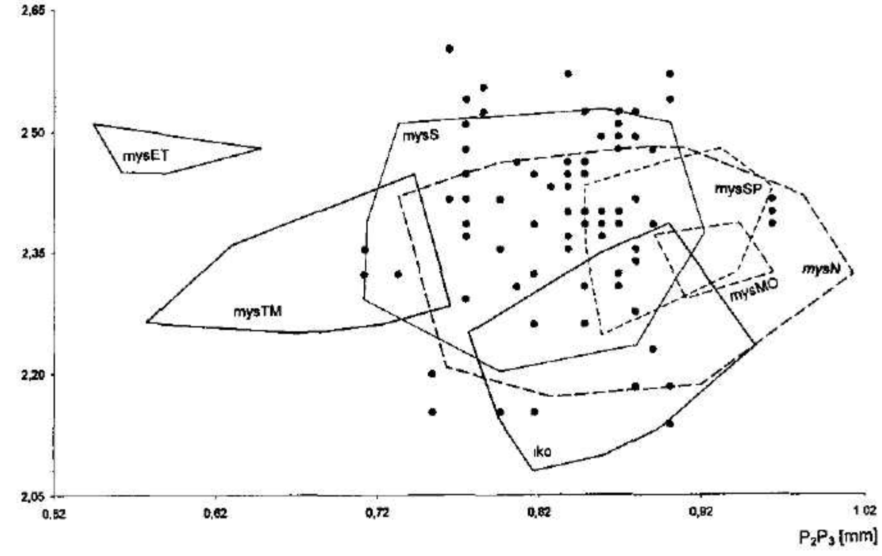


Fig 37 A comparison of the length of lower premolar-row (P_2P_3) versus upper molar-row (M^1M^2) Polygons – samples with low variation, dots – Balkan population of *Myotis mystacinus* s. l. For abbreviations see p 336

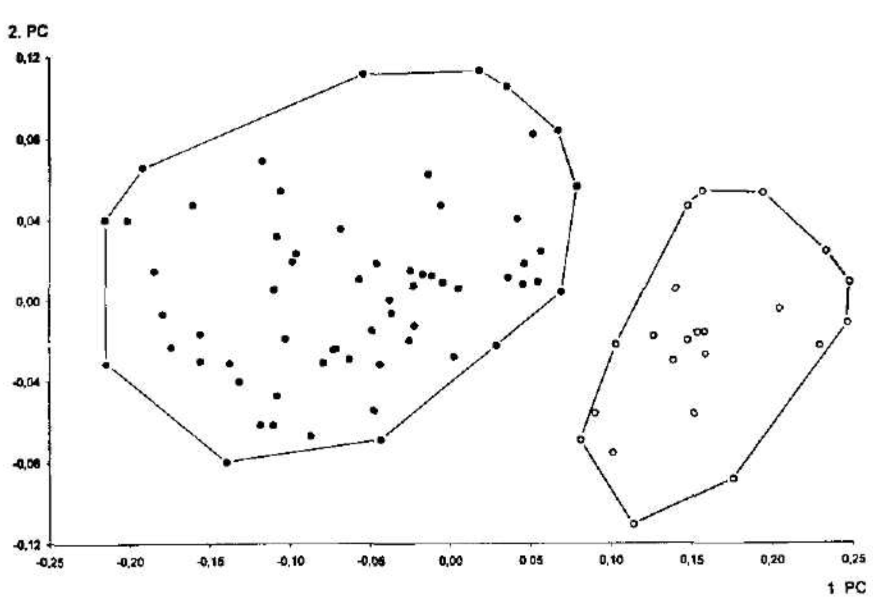
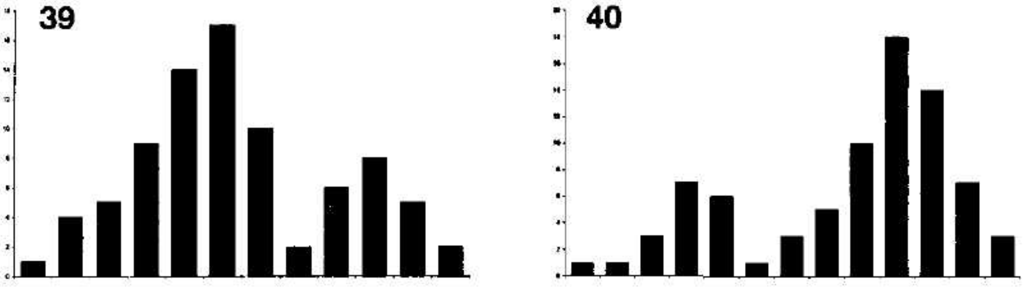


Fig. 38. Principal component analysis of the Balkan sample of *Myotis mystacinus* s. l. *M. brandtii* was not included in the analysis. Open circles – specimens previously identified as members of the "northern" populations of *M. mystacinus* s. l., closed circles – specimens previously identified as members of the "southern" population of *M. mystacinus* s. l.

that the "nothern" and "southern" populations of *M. mystacinus* s. l. occur sympatrically in the Balkans. This agrees with the presence of two types of bacula in the Balkan sample of *M. mystacinus* s. l. (see Figs 19 and 27) and with dental characters (see Fig. 37).

This conclusion is supported also by the principal component analysis of the Balkan sample of *M. mystacinus* s. l. (Fig. 38). The comparison of PC I and PC II formed two clusters of specimens (1. PC = 49.3% of variation [reflects especially the dimensions LCr, LCb, LMd, and ACin], 2. PC = 9.7% [P^2P^3, LP^3, P_2P_3, LP_3]), which correspond to the "northern" and "southern" populations of *M. mystacinus* s. l., respectively. The frequency of scores around the regression line ($y = -0.364x$) exhibits a distinctly bimodal distribution (Fig. 39) similar to that around the regression of the height of cingular cusp of P^4 on the skull length, i. e. ACin = 0.53–0.038LCr, as shown in Fig. 40. Both the cases clearly demonstrate that two different phenotypic entities occur here in sympatry. The lack of marked overlap of the two phenotypic states (as seen in Figs 39, 40) indicates, that these entities can be considered separate species. It is possible to identify these entities as the "northern" and "southern" phenotype, as defined above. The "northern" phenotype is characterized by small to middle-sized skull, middle-high mesiopalatal cingular cusp of P^4, and rather round cingulum of the upper canine. "Southern" phenotype is characterized by large skull, low or absent mesiopalatal cingular cusp of P^4, and rather narrow upper canine.

It is possible to summarize, that the analysis of the Balkan sample of *M. mystacinus* s. l. showed, that two phenotypic forms – called "northern" and "southern" populations of *M. mystacinus* s. l. –



Figs 39, 40 Plots of score frequencies of the Balkan sample of *Myotis mystacinus* s. l. 39 – frequency of scores around the regression line of the 1st principal component on the 2nd principal component ($y = -0.364x$), see Fig. 38. 40 – frequency of scores around the regression line of the height of mesiopalatal cingular cusp of P^4 on the skull length ($y = -0.038x + 0.53$), see Fig. 35

sympatrically occur in the Balkans. The "northern" population includes the "topotype population" of *Myotis mystacinus* (Kuhl, 1817), i. e. Central Europe, so that the Balkan individuals which exhibit the "northern" phenotype can be identified as *M. mystacinus* s. s. On the other hand, Balkan individuals which exhibit the "southern" phenotype belong – together with the bats from Dalmatia, Ukraine and Lower Volga region – to a different species

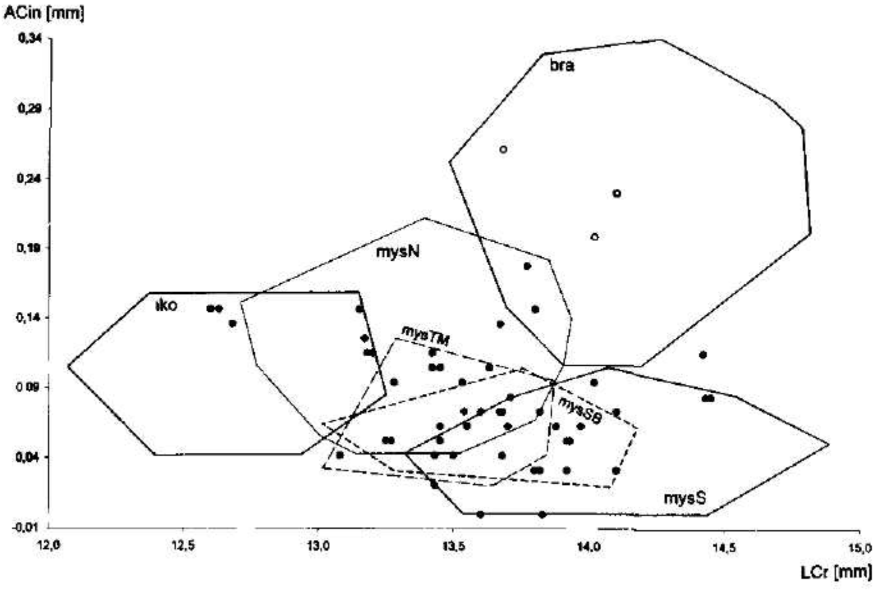


Fig. 41 A comparison of the greatest length of skull (LCr) versus height of mesiopalatal cingular cusp of P^4 (ACin). Polygons – samples with low variation, symbols – Caucasus population (circles – *Myotis brandtii*, dots – *M. mystacinus* s. l. except for the sample SB which is indicated by a polygon). For abbreviations see p. 336

Western Mediterranean population
Western Mediterranean samples of *M. mystacinus* s. l. from Spain and Morocco (SP, MO) belong to the type of samples with low variability, but differ from the remaining samples from the *M. mystacinus* group in some characters. These differences are apparent from the statistical data (Figs 3–14), and from graphical comparisons (Figs 35–37). In particular, western Mediterranean bats have larger skull (Figs 3–5), longer forearm (LAt, Fig. 12), and different upper canine (Fig. 36). This tooth is very long (as in "southern" populations, LCn, Fig. 9), and extremely wide (more than in any other sample, LaCn, Fig. 10), reaching thus values of RCn comparable with those of the "northern" populations (Fig. 11). Also other important characters, such as height of the cingulum of P^4, and length of premolar- and molar-rows (Figs 35, 37) point toward the "northern" population of *M. mystacinus* s. l. Unfortunately, no baculum from western Mediterranean bats was available for study. The western Mediterranean population is clearly distinct within the *M. mystacinus* group, being close to the "northern" population of *M. mystacinus* s. l.

Caucasus population
The Caucasus populations – as defined here – consists of four samples, incl. *M. brandtii* (CA), and *M. mystacinus* s. l. from Ciscaucasia (CC), Sevan Lake basin (SB) and the Great Armenia and Transcaucasia (TC). The samples are compared in Figs 41–44 with selected populations, incl. *M. ikonnikovi*, "northern" samples of *M. brandtii* (CE, BT, UR), and "northern", "southern" and "eastern" samples of *M. mystacinus* s. l.

The comparison resulted in two basic observations: (1) Samples are distributed as in the Balkans, and correspond to *M. brandtii*, and to the "northern" and "southern" population of *M. mystacinus*

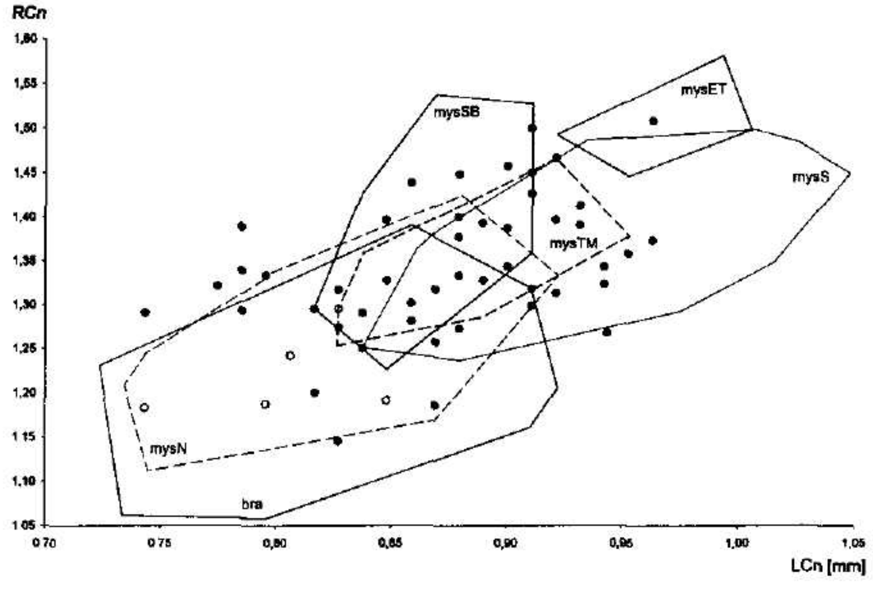


Fig. 42. A comparison of the length (LCn) versus relative width (RCn) of the upper canine. Polygons – samples with low variation, symbols – Caucasus population (circles – *Myotis brandtii*, dots – *M. mystacinus* s. l. except for the sample SB which is indicated by a polygon). For abbreviations see p. 336.

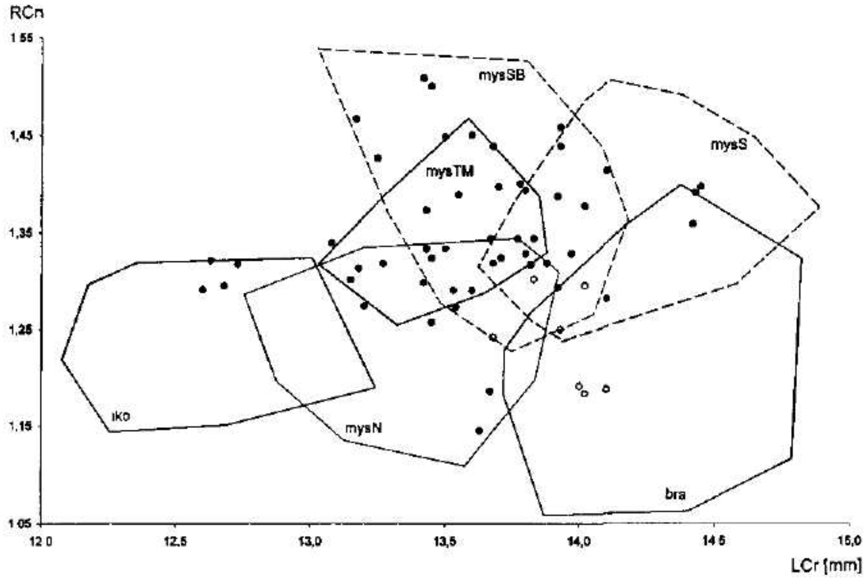


Fig 43 A comparison of the greatest length of skull (LCr) versus relative width of the upper canine (RCn) Polygons – samples with low variation, symbols – Caucasus population (circles – *Myotis brandtii*, dots – *M mystacinus* s l except for the sample SB which is indicated by a polygon) For abbreviations see p 336

s. l., respectively. As shown above, the latter two "populations" belong to two different species. (2) Some individuals fall in clusters, which are different from the three above mentioned ones. Bats from one of these clusters correspond in size and morphology to the bats from Turkestan (TM, ET), while the bats from the Sevan Lake basin do not correspond to any other population. Although the number of specimens is too small for a thorough statistical analysis, the morphological observation is sufficient for conclusion, that five morphotypes of whiskered bats occur in the Caucasus region.

In addition to the three forms, which sympatrically occur also in the Balkans, two other forms do not occur more to the west. The population from the Sevan Lake basin is characterized by rather large skull, rather low mesiopalatal cingular cusp of P^4 (both characters being intermediate between the "northern" and "southern" form of *M. mystacinus* s. l.), extremely narrow and short upper canine, very short premolar- and molar-row (the molar-row being similar to that of *M. ikonnikovi* in length), and unusually large wing (Figs 12–14). Each character overlaps with the values of some other samples, but the combination of characters is unique, which indicates, that the sample represents an independent form.

The last type of whiskered bats from Caucasus region corresponds in size and morphology with the population TM, which is characterized by middle-sized skull, rather low cingular cusp of P^4, very narrow upper canine, very short premolar-row, relatively long molar-row, and middle-sized wing.

This study revealed the existence in the geographically diverse Caucasus region of five phenotypes which belong to the *M. mystacinus* group. All of them occur sympatrically in the southern part of this region, particularly in the Armenian Highlands and in Transcaucasia (Fig. 45). *M brandtii* and "northern", "southern" and "eastern" phenotypes of *M. mystacinus* s. l. are characterized also by the morphology of bacula, while bacula of bats of the fifth phenotype (Sevan Lake basin population of *M mystacinus* s l) were not available for study

Conclusions

The following conclusions can be drawn on the basis of a morphometrical study of external, cranial and dental characters, and on the basis of a comparative morphological study of the teeth and baculum

(1) No differences were found in the West Palearctic population of *M brandtii* Formerly known characters and the definition of the species were confirmed Clinal changes in size on north-south and/or west-east gradients were found for some characters

(2) The validity of *M ikonnikovi* was confirmed on the basis of metrical, dental and penial characters It was found, that this species is closely related to *M mystacinus*, not to the Oriental *M muricola*, which very probably belongs to another species group or subgroup *M ikonnikovi* was not recorded in the western Palearctic

(3) Three basic morphotypes were distinguished in *M mystacinus* in its current understanding (s l) on the basis of metrical, dental and penial characters The three morphotypes differ in geographic distribution, so that the following forms were recognized "northern" form (Central and north-eastern Europe), "southern" form (south-eastern Europe), and "eastern" form (Middle and Central Asia)

(4) Three forms of *M mystacinus* group were found to occur sympatrically in the northern Balkans *M brandtii*, and two forms of *M mystacinus* s l , which correspond to the "northern" and "southern" morphotype (see point 3 above) Both of them thus deserved separation at the species rank

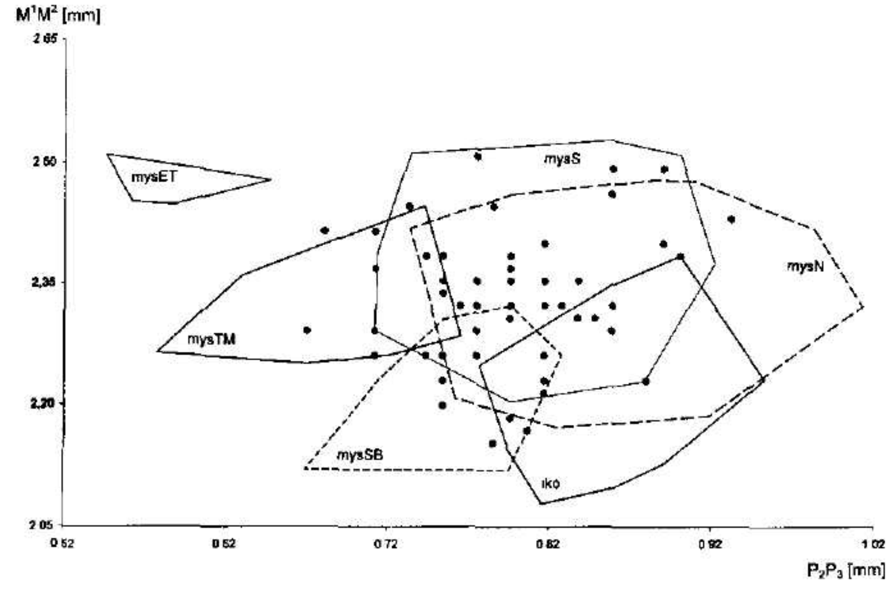


Fig 44 A comparison of the length of lower premolar-row (P_2P_3) versus upper molar row (M^1M^2) Polygons samples with low variation, dots – Caucasus population of ***Myotis mystacinus*** s l except for the sample SB which is indicated by a polygon For abbreviations see p 336

Tab. 2 Differences in some characters of individual forms of *Myotis mystacinus* group in the western Palearctic and of *M. ikonnikovi*. Abbreviations of taxa: *brandtii* – *M. brandtii brandtii*, *ikonniko* – *M. ikonnikovi*, *mystacin* – *M. mystacinus mystacinus* and *M. m. caucasicus* ssp. n., *occident* – *M. mystacinus occidentalis* ssp. n., *aurascen* – *M. aurascens*, *hajastan* – *M. hajastanicus*, *transcas* – *M. nipalensis transcaspicus*

	brandtii	*ikonniko*	*mystacin*	*occident*	*aurascen*	*hajastan*	*transcas*
large skull	++	– –	±	+	++	+	±
long premolar tooth-row	++	+	+	++	±	–	– –
long molar tooth-row	++	– –	±	±	++	– –	±
high P^4 cingular cusp	++	±	±	±	– –	–	–
long upper canine	– –	– –	– –	±	++	±	±
relative wide upper canine	++	++	++	++	–	– –	– –
presence of paraconules	+	–	–	–	–	–	–
presence of paralophs	+	±	±	±	±	±	+
presence of metaconules	+	±	±	±	+	±	+
presence of metalophs	+	–	–	–	–	–	–
large wing	+	±	±	+	+	++	±

The same condition was found also in the northern part of the Caucasus region, and in the region of the middle flow of the Volga river.

(5) Another form of *M. mystacinus* s. l. was found in the western Mediterranean, similar in some respect to the "northern" morphotype.

(6) In the southern part of the Caucasus region, the following five forms from the *M. mystacinus* group were found to occur sympatrically: *M. brandtii*, "northern", "southern" and "eastern" morphotypes of *M. mystacinus* s. l., and a separate form related to the "eastern" morphotype of *M. mystacinus* s. l., which was found only in the Sevan Lake basin (Armenia).

TAXONOMIC PART

As mentioned above, five forms from the *M. mystacinus* group occur in the western Palearctic, which should be separated at the species level, because they occur in sympatry, and a few further forms, which can be defined morphologically, but which occur in allopatry or parapatry (cf. Tab. 2). As mentioned above, *M. ikonnikovi* is a valid species from eastern Palearctic, and the name cannot be applied to any west Palearctic form. Overall, 26 names were proposed within the group under study on the basis of specimens from the Palearctic region (except for Japan), viz. *Vespertilio mystacinus* Kuhl, 1817; *Vespertilio collaris* Schinz, 1821; *Vespertilio humeralis* Baillon, 1834; *Vespertilio schinzii* Brehm, 1837; *Vespertilio schrankii* Wagner, 1843, *Vespertilio Brandtii* Eversmann, 1845; *Brachyotus mystacinus* var. *aureus* Koch, 1865; *Brachyotus mystacinus* var. *nigricans* Koch, 1865; *Brachyotus mystacinus* var. *rufofuscus* Koch, 1865; *Vespertilio mystacinus* var. *nigricans* Fatio, 1869; *Vespertilio lugubris* Fatio, 1869; *Vespertilio mystacinus* var. *nigrofuscus* Fitzinger, 1871; *Vespertilio nipalensis* Dobson, 1871, *Vespertilio mystacinus sibiricus* Kaščenko, 1905; *Myotis meinertzhageni* Thomas, 1926; *Myotis mystacinus przewalskii* Bobrinskoj, 1926; *Myotis mystacinus gracilis* Ognev, 1927; *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928; *Myotis mystacinus kukunorensis* Bobrinskoj, 1929; *Myotis mystacinus sogdianus* Kuzjakin, 1934; *Myotis mystacinus aurascens* Kusjakin, 1935; *Myotis mystacinus pamirensis* Kusjakin, 1935; *Myotis mystacinus bulgaricus* Heinrich, 1936; *Myotis mystacinus hajastanicus* Argyropulo, 1939; *Myotis coluotus* Kostroň, 1943; *Myotis mystacinus popovi* Strelkov, 1983; *Myotis mystacinus mongolicus* Kruskop et Borissenko, 1996. We restudied all existing type materials, with the exception of that of *nipalensis*, and compared it with the characters of the above defined forms.

Of the five forms, *Myotis brandtii* (Eversmann, 1845) is a well defined species, of which *coluotus*, *gracilis*, and *sibiricus* were reidentified as synonyms (Ognev 1928, Strelkov 1983a, Tiunov 1997, Benda 1999). *M. mystacinus hajastanicus* Argyropulo, 1939 was described from the Sevan Lake basin in Armenia, and the name is thus applicable to the local population (SB). The forms *aureus*, *collaris*, *humeralis*, *nigricans* Koch, 1865, *nigrofuscus*, *rufofuscus*, *schinzii*, and *schrankii* are synonyms of either *M. mystacinus* s. s. or *M. brandtii*, but neither their diagnoses, nor their types are available (see a review by Benda 1999). As already mentioned above in a chapter on the Balkan population, the "northern" form agrees in distribution and morphology with "topotype population" of *Myotis mystacinus* (Kuhl, 1817). Also the revised types of *Vespertilio mystacinus* var. *nigricans* Fatio, 1869 and *Vespertilio lugubris* Fatio, 1869 respectively, agree in morphology with this population.

Characters of the "southern" population of *M. mystacinus* s. l., which occurs in south-eastern Europe from Dalmatia till lower Volga river and the Great Armenia, are exhibited also in the types of *aurascens*, *bulgaricus*, *popovi*, and also of *mongolicus* from eastern Palearctic. The earliest of these names is *Myotis mystacinus aurascens* Kusjakin, 1935, which should be used for this newly defined SE-European species, which should henceforth be known as *M. aurascens*. The types of

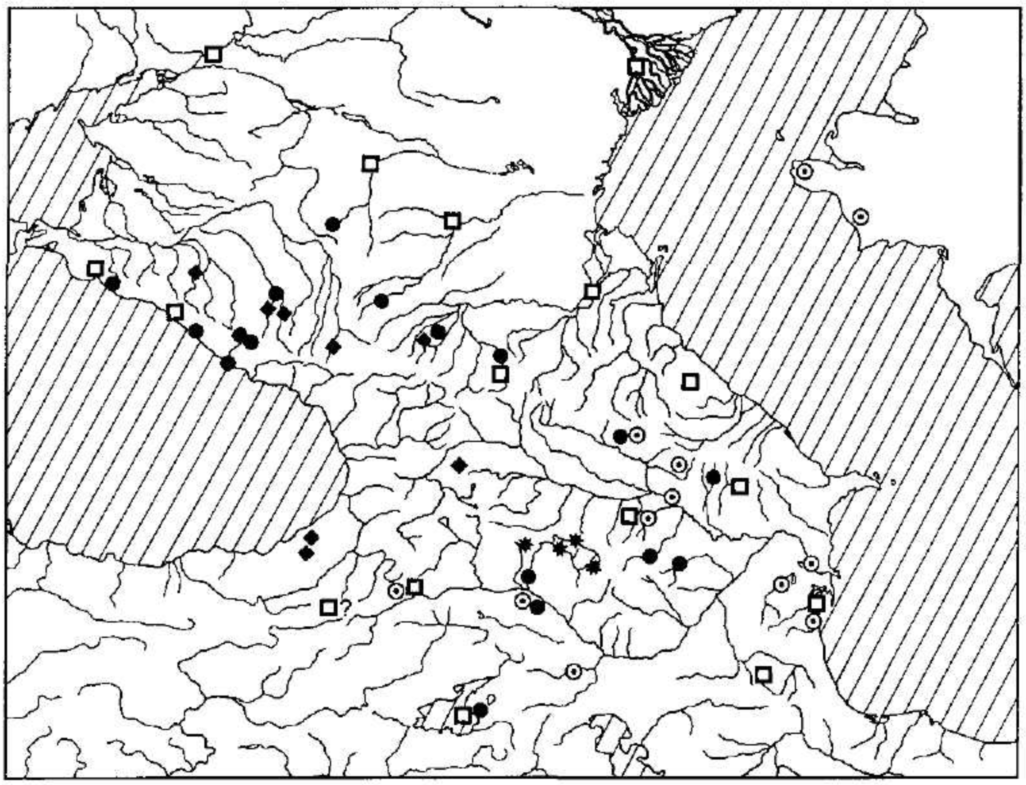


Fig. 45. Distribution of individual phenotypes (species) of *Myotis mystacinus* group in the Caucasus region. Based on revised specimens (see App. II) and, in the case of *M. brandtii*, also on published data (Benda & Horaček 1998, Ilyin et al. 1998, Strelkov 1983b). Explanantion: ◆ – *M. brandtii*, ● – *M. mystacinus caucasicus* ssp. n., ☐ – *M. aurascens*, ✱ – *M. hajastanicus*, ⊙ – *M. nipalensis*

the remaining forms originated from the area of the "eastern" form of *M. mystacinus* s. l., including *kukunorensis*, *meinertzhageni*, *nipalensis*, *pamirensis*, *przewalskii*, *sogdianus*, and *transcaspicus*, and all their revised types agree in characters with the latter form. The earliest available name is here *Vespertilio nipalensis* Dobson, 1871. We did not revise the type specimen of this form, which is deposited in the Indian Museum in Calcutta, India (Dobson 1876), but we studied relevant material from other collections (App. II). Hence, we call here preliminarily the newly defined "eastern" species from the *M. mystacinus* group as *M. nipalensis*. Another taxon, the revision of which could result in nomenclatural changes in the "eastern" population of *M. mystacinus* s. l., is *Vespertilio Davidii* Peters, 1869. See Discussion for more details.

***Myotis brandtii brandtii* (Eversmann, 1845)**
(Figs 15–17, 46, 49, 53, 56)

Vespertilio Brandtii Eversmann, 1845 505

Vespertilio mystacinus sibiricus Kaščenko, 1905 24–25, Ognev 1928: 447–449; Ellerman & Morrison-Scott 1951 139, Pavlinov & Rossolimo 1987 37

Myotis mystacinus mystacinus [partim] Bianchi 1917: 80; Bobrinskoj 1929 224, Kuzjakin 1950 279, Kuzjakin 1965 96

Myotis mystacinus brandtii. Ognev 1927: 145, Ognev 1928. 447–452; Kuzjakin 1934: 321; Stubbe & Chotolchu 1968 27–31

Myotis coluotus Kostroň, 1943 1, Benda 1999 14–18

Myotis mystacinus brandtii Ellerman & Morrison-Scott 1951. 139; Abelencev et al 1956: 341; Topál 1958 333, Strelkov 1963 166, Hanak 1965 354–366, Mošansky & Gaisler 1965. 261; Feriancová-Masárová & Hanák 84, Hanák 1967 201

Myotis brandtii Hanak 1970: 43, Gauckler & Kraus 1970: 113–124, Horáček et al. 1974: 22, Corbet 1978, 47, etc

Myotis brandtii Hanák 1971 175 184, Baagøe 1973: 191–215, Benda 1999: 5–23; etc

Myotis brandtii brandtii Strelkov 1983a: 259; Koopman 1994 103.

TYPE MATERIAL EXAMINED **Lectotype** *sex unknown, ZIN 41687, skull and mounted dry skin, Spask, ca 100 km ENE* to Orenburg; 29 June 1842, leg E. Eversmann **Paralectotypes**. male and female, ZIN 41685, 41686, mounted skins (skulls not extracted); the same locality as lectotype, July 1842, leg. E. Eversmann The syntypical series was identified, and the lectotype was designed by Baranova et al (1981: 13)

RESTRICTED TYPE LOCALITY. Spask (= Спасское [Spasskoe]), Bol'šoj Ik river, Orenburg Region, Russia (Baranova et al. 1981).

DESCRIPTION. The largest bat of the group. Skull middle sized to large (LCr 13.5–14.8 mm), with a rather flat frontal and parietal parts and convex occipital region (Figs 46, 49, 80); upper canine short (mesiodistally, LCn 0.72–0.92 mm), with round cingulum (RCn 1.05–1.39), crown with pseudotriangular basis, large mesiodistal concavity and deep labiodistal groove, mesial surface convex with mesiolabial groove (Fig. 53); P^4 has a medium to very high cusp on the mesiopalatal edge of the cingulum (ACin 0.11–0.34 mm), premolar- and molar-row long (Figs 6, 7), P^3 and P_3 rather robust and high, P^3 mostly reaches $^{2}/_{3}$ of P^2 in height, and is located in the teeth-row (Fig. 53); paralophs, metaconules and metalophs on molars almost always present, paraconules present in most cases (Tab. 1, see also Tupinier & Aellen 1978, Menu & Popelard 1987, etc.); I^2 with shallow groove or tiny protuberance on the palatal edge of cingulum (Fig. 67). Distal part of penis club-shaped (the same as in Fig. 79); baculum large and broad, length 0.80–1.07 mm, proximal width 0.51–0.83 mm (Figs 15–17). Colour of adults brownish, on the back light brownish to brownish, proximal parts of back hair dark brown, distal ends of back hair brown with golden, ochre or orange hinge; belly greyish, proximal parts of belly hair black-brown, distal ends of belly hair grey to brownish grey, throat darker than belly. Hairless parts brown to dark brown, basis of the ear and some parts of the snout can be light. Wing medium large to large (LAt 32.2–37.1 mm). Size and selected statistical parameters are shown in App. III, Tabs 9–11.

DISTRIBUTION. *Myotis brandtii brandtii* is distributed in the western Palearctic in the whole zone of northern forests and in the northern and eastern part of the zone of European mixed forests. The range forms a broad stripe from the island of Great Britain via northern France and Central Europe to eastern Europe (and further to the east). Northern border of the European distribution corresponds with the northern border of the forest zone in central Sweden and Finland (see Mitchel-Jones et al. 1999). Southern border of regular distribution pass western France (Côte d'Or), southern slopes of the Alps and the Carpathians to Ural Mts. Southernmost records of the continuous range come from the mountains of Slovenia (two localities; Kryštufek & Červeny 1997), Croatia (three localities; Tvrtković in litt.) and southern Hungary (Mitchell-Jones et al. 1999). *M. b. brandtii* is very probably distributed also in the southern Carpathians in Romania, but no records are available. Hackethal (1982) mentioned that three specimens were recorded in Romanian Carpathians, but did not specify where exactly.

Outside the continuous range are records of *M. b. brandtii* from central Italy (Zava & Violani 1992), from the Balkans and from the Caucasus region. In Romania, only a single record of the species is known from Dobrogea (Grimmberger 1993). In the Balkans, most records come from the Bulgarian mountains: Rhodope Mts. (Horáček et al. 1974), western part of Balkan Mts. (Ivanova 1998, Pandurska & Beshkov 1998), and Rila Mts. (Ivanova, unpubl. record); one record comes from Montenegro (Ćakor; Petrov 1967, rev. Strelkov 1983a). A probably isolated population inhabits the forest zone of the Caucasus region (see Fig. 45), i. e. western part of the main range of the Greater Caucasus Mts., westernmost part of the Lesser Caucasus Mts. and the East Pontic Mts. (Albayrak 1991, Steiner & Gaisler 1994, Strelkov 1983b, Ilyin et al. 1998).

Myotis mystacinus mystacinus (Kuhl, 1817)

(Figs 19, 20, 47, 50, 55, 56, 60, 61, 67, 68)

Vespertilio mystacinus Kuhl, 1817: 58; Kuhl 1819: 202.

Vespertilio mystacinus var. *nigricans* Fatio, 1869 = *Vespertilio lugubris* Fatio, 1869: Miller 1912: 169, Ellerman & Morrison-Scott 1951: 139; Baud 1977: 207.

Myotis mystacinus mystacinus [partim]: Heinrich 1936: 38; Kuzjakin 1950: 279, Ellerman & Morrison-Scott 1951: 139, Abelencev et al. 1956: 341; Strelkov 1963: 165; Kuzjakin 1965: 96; Hanák 1965: 353–366; Mošanský & Gaisler 1965: 260; Feriancová-Masárová & Hanák 1965: 81–83; Corbet 1978: 47; Strelkov 1983a: 260, Koopman 1994: 103.

Myotis ikonnikovi: Abelencev 1950: 66; Abelencev et al. 1956: 334, Kvartirnikov 1957: 63, Beron 1961: 64, Atanassov & Peschev 1963: 103; Valenciuc 1971: 333–334, Helversen 1989b: 56.

TYPE MATERIAL EXAMINED. Syntypes of *Myotis mystacinus* var. *nigricans* Fatio, 1869 = *Vespertilio lugubris* Fatio, 1869. **Lectotype** (by present designation). sex unknown (adult specimen), MNHG 713.21, skull (partly damaged) and dry skin, Rosenlaui, Bern, Switzerland; 1863, leg. M. V. Fatio. **Paralectotype**: sex unknown (juvenile specimen), MNHG 712.30, dry skin (skull not extracted); Rosenlaui, Bern, Switzerland; 1863, leg. M. V. Fatio.

TYPE LOCALITY. Germany (Kuhl 1817, 1819, Ellerman & Morrison-Sott 1951, Kuzjakin 1950, 1965, Corbet 1978); restricted to Hessen, Germany (Gauckler & Kraus 1970).

DESCRIPTION. Smallest bat from the group in the western Palearctic; skull small to middle sized (LCr 12.7–13.9 mm), with convex frontal and parietal parts and rather flat occipital region (Figs 47, 50, 80); upper canine short (mesiodistally, LCn 0.73–0.94 mm), cingulum triangular to rounded (RCn 1.11–1.37), crown with pseudotriangular basis, with a large mesiodistal concavity and a small labiodistal concavity, mesial surface convex, sometimes with a shallow groove (Figs 55, 56); P^4 always has low to middle high cusp on the mesiopalatal edge of the cingulum (ACin 0.04–0.21 mm), premolar- and molar-row long (Figs 6, 7), P^3 and P_3 middle sized to large, P^3 mostly reaches $^1/_2$ of P^2 *in height, and is located in the axis of the teeth-row (Figs 55, 56); paraconules on molars almost* always absent, metalophs mostly absent (Tab. 1), approximately a half of specimens have depeloped metaconules, paralophs are often present (Figs 60–61); I^2 mostly has a low protuberance on the palatal edge of cingulum (Fig. 69), in some cases, the protuberance is highly developed and almost equals in size the lateral (largest) cusp (Fig. 68). The whole penis is equally broad, baculum narrow, with less developed "wings" (Figs 19–20). Colour of adults dark brown, on the back brown to black-brown, proximal parts of back hair dark brown to black, distal ends of back hair dark brown to black-brown, sometimes with golden or silver hinge; belly hair greyish, proximal parts of belly hair black-brown, distal ends of belly hair grey to brown-grey, hair on throat is darker than on belly. Hairless parts are dark brown, black-brown to black, basis of the ear heavily pigmented. Wing very small to middle sized (LAt 30.5–35.7 mm). Size and selected statistical parameters are listed in App. III, Tabs 1–3, 6.

Distribution. *M. m. mystacinus* is distributed in the whole area of the species in the western part of the Palearctic with the exception of the western Mediterranean and the Caucasus region. This area includes the whole Central Europe ("type population"), incl. the Alps and Carpathians. In the west it includes British Islands, southernmost part of Norway, southern Sweden and Finland till St. Petersburg region (Mitchell-Jones et al. 1999). It inhabits northern Balkans, especially higher areas of Bulgaria, Greece and Macedonia. The range continues from the Central Europe in central Russia and to the Ural Mts., which are probably the eastern borders of the subspecies as well as the whole species (comp. Strelkov 1983b). The southern border in eastern Europe corresponds probably with the border between forests and steppe running from Moldavia to the Ural Mts. At the latter line, the species is sympatric with *M. aurascens* (two localities at the middle flow of the Volga river, see App. II). Unknown is the distribution in Italy south of the Alps, where the species may be sympatric with *M. aurascens*. Two revised specimens from Corsica very probably also belong to *M. m. mystacinus* (cf. Kahmann & Goerner 1956).

Myotis mystacinus occidentalis Benda ssp. n.

Myotis mystacinus mystacinus. Corbet 1978: 47; Koopman 1994: 103

Type material. **Holotype**. female, SMF 19664, skull and dry skin; Linares de Riofrio, Salamanca, Spain, 18 May 1960, leg. H. Grün. **Paratypes** (13): four males and nine females, SMF 16183, 17828, 19665–19667, 20696–206700, 21547, 21548, 22455, skulls and dry skins; Linares de Riofrio, Salamanca, Spain, 21 Aug 1957, 4 June 1956, 19 and 21 May 1960, 17 and 28 July 1961, 10 and 11 July 1962, 30 June 1963, leg. H. Grun

Type locality. Linares de Riofrio, Salamanca Prov., western Spain.

Description. In most characters, this form is identical with the nominotypical form. Middle sized bat of the group; for dimensions see App. *III*, Tab. *1*. Skull middle sized (LCr 13.2–14.1 mm [M 13.77 mm]), with convex frontal region; upper canine long (mesiodistally, LCn 0.85–1.01 mm [M 0.92 mm]) and very broad (LaCn 0.69–0.81 mm [M 0.74 mm]), cingulum rounded (RCn 1.14–1.37 [M 1.249]), crown with pseudotriangular basis, large mesiodistal concavity and a smaller labiodistal concavity, mesial surface slightly convex, sometimes with a groove; P^4 always has a low to middle high cusp on the mesiopalatal surface of cingulum (ACin 0.04–0.15 mm [M 0.094 mm]), premolar and molar-row long (Figs 6, 7), P^3 and P_3 middle robust, located in the teeth-row; molars always lack paraconules, metalophs are mostly absent (Tab. 1). Colour of adults rather light, back brown, proximal parts of back hair dark brown, distal ends of back hair light with ochre hinge. Wing small to middle sized (LAt 32.8–36.6 [M 34.73 mm]).

Differential diagnosis. *M. m. occidentalis* ssp. n. agrees with the nominotypical subspecies in most characters, but differs from it in being larger (Figs 3–5, 35, 37), it is the largest known form of *M. mystacinus* s. s., and in having longer and more robust rostrum, markedly more robust canines (Figs 9, 10, 36), which are in mean by 0.08 mm longer and by 0.07 mm wider than in *M. m. mystacinus*, and somewhat lighter coloration of the pelage.

DISTRIBUTION. *M. m occidentalis* ssp. n. occurs in the Iberian Peninsula. Overall, 13 localities are known, incl. the type locality and two another localities from which we revised the material (see App. II), and other localities summarized by Fernandez & Ibañez (1989) and/or Ibañez et al. (1992). In addition, the population of *M. mystacinus*, which inhabits northern Morocco (Panouse 1953, Aulagnier & Destre 1985, Ibañez 1988), probably belongs to this subspecies, because not substantial differences were found between them (Figs 3–8, 12–14, 37, App. III, Tab. 1).

Myotis mystacinus caucasicus Tsytsulina ssp. n.

(Figs 21, 22)

Myotis mystacinus mystacinus [partim]. Kuzjakin 1950: 279, Kuzjakin 1965: 96, Corbet 1978: 47, Koopman 1994: 103

Myotis mystacinus aurascens [partim]. Abelencev et al. 1956: 341, Strelkov 1963: 166, Strelkov 1983a: 263, Tsytsulina 1999: 65

Myotis ikonnikovi Kormilicina 1977: 55–56

TYPE MATERIAL. **Holotype**: male, ZIN 83623, skin and skull, kordon Kiša, Northern Part of the Caucasus State Reserve, Krasnodar Region, Russia; 19 June 1998, coll. B. S. Tuniev. **Paratypes** (2): female, ZIN 83008, skin and skull, Imeretinskaja lowland, Adler, Krasnodar Region, Russia; 16 July 1997, coll. K. Tsytsulina. Male, ZIN 833771, skin and skull, Rhožkova cave, Ahmet-skala mountain ridge, Psebaj village environs, Krasnodar Region, Russia, January 1998, coll. S. V. Gazarjan

TYPE LOCALITY. Kiša forester-lodge [кордон Киша], Northern Part of the Caucasus State Reserve [Кавказский заповедник], Krasnodar Region, north-western part of the Greater Caucasus Mts., southern Russia.

DESCRIPTION. Similar to the nominotypical form in most characters. Smallest bat of the group in the western Palearctic (for dimensions see App. III, Tab. 8); skull small to middle sized (LCr 12.6–13.7 mm [M 13.245 mm]), with frontal region convex; upper canine short (mesiodistally LCn 0.74–0.94 mm [M 0.852 mm]) with rounded cingulum (RCn 1.14–1.34 [M 1.275]), crown with pseudotriangular basis, large mesiodistal concavity and a smaller labiodistal concavity, mesial surface flat or slightly convex, somewhat with a groove, P^4 always with a low or medium high cusp on the mesiopalatal edge of cingulum (ACin 0.04–0.21 mm [M 0.111 mm]), premolar- and molar-row long (Figs 6, 7), P^3 and P_3 middle robust, located in the teeth-row; paraconules and metalophs on molars absent, paralophs generally present. For other dimensions see App. III, Tab. 8. Baculum middle-sized (maximum length 0.60–0.73 mm); the "head" on the distal epiphysis is large and "wings" are well developed with wide margins (Figs 21, 22). Colour of adults dark brown, back brown to black-brown, proximal parts of back hair dark brown to black, distal ends of back hair dark brown to black-brown, sometimes with golden or silver hinge; belly greyish, proximal parts of belly hair black-brown, distal ends of belly hair grey to brown-grey, throat darker than belly. Hairless parts dark brown, black-brown to black, basis of the ear dark pigmented. Wing small to middle-sized (LAt 33.7–35.5 mm [M 34.83 mm]).

DIFFERENTIAL DIAGNOSIS. *M. m. caucasicus* ssp. n. agrees in most characters with the nominotypical subspecies, from which it differs in the absence of a protuberance on the palatal edge of I^2, and – most importantly – in the structure of baculum (see Description).

DISTRIBUTION. *M. m. caucasicus* ssp. n. is distributed in the Caucasus region (Fig. 45), from Greater Caucasus Mts. to the Armenian Highlands. Most of the records came from the mountain forest zone and from the foothills of the Greater Caucasus Mts. from its westernmost edge (Novorossijsk) to northern Azerbaijan (Kutkašan). Other records are available from the Lesser Caucasus Mts. and from the central part of Armenian Highlands (Van). This is probably the southern border both of the subspecies *M. m. caucasicus* ssp. n., and of the species as a whole.

Myotis aurascens Kusjakin, 1935 stat. n.

(Figs 24–30, 48, 51, 57, 63, 69, 72, 73, 76)

Myotis mystacinus aurascens Kusjakin, 1935: 432, Ellerman & Morrison-Scott 1951: 140

Myotis mystacinus aurascens [partim] Abelencev et al. 1956: 341; Strelkov 1963: 166; Strelkov 1983a: 263; Tsytsulina 1999. 65.

Myotis mystacinus bulgaricus Heinrich, 1936: 38; Ellerman & Morrison-Scott 1951: 140; Atanassov & Peschev 1963: 103; **syn. n.**

Myotis mystacinus brandtii: Martino 1939: 87; Hanák 1965. 362 [partim]

Myotis mystacinus mystacinus [partim]: Kuzjakin 1950: 279; Kuzjakin 1965. 96; Hanák 1965. 362; Đulić & Tortić 1968. 5, Corbet 1978: 47; Koopman 1994. 103; etc.

Myotis mystacinus brandtii? Đulić & Tortić 1968: 5

Myotis "mystacinus" przewalskii [partim]: Stubbe & Chotolchu 1968: 31–35.

Myotis mystacinus popovi Strelkov, 1983a: 262–263; Benda 1999: 10–12, Tsytsulina 1999: 65, **syn. n.**

Myotis sp. A Volleth 1987: 188–195.

Myotis przewalskii [partim]. Helversen 1989a: 12–13; Helversen 1989b: 56–57

Myotis mystacinus hajastanicus Albayrak 1991: 118 [partim]

TYPE MATERIAL EXAMINED. *Myotis mystacinus aurascens* Kusjakin, 1935. **holotype**: male, ZMMU S9266, skull and dry skin; Kurkužin village near Vladikavkaz, Russia; 11 May 1928, leg. A. Radišev. *Myotis mystacinus bulgaricus* Heinrich, 1936. **holotype**: female, BZM 47264, skull and dry skin; Philippopel [= Plovdiv], Bulgaria, 3 Sept 1935, leg. G. Heinrich. **Paratypes** (3): Two males, BZM 47265, 47266, skulls and dry skins, Philippopel, Bulgaria; 21 Sept. 1935, leg. G. Heinrich. Male, MTD B13208, skull and dry skin; Philippopel, Bulgaria, 10 Sept 1935, leg. G. Heinrich. *Myotis mystacinus popovi* Strelkov, 1983: **holotype**. male, ZIN 45249, skull and dry skin, Krym (= Crimea), Kerčenskij poluostrov Pen., vicinity of Kamenskoe vill., Ukraine; Febr. 1961, leg. A. Konstantinov. **Paratypes** (9): female, sex unknown, ZIN 8057, 9189, skulls; Tatakoj, n. Simferopol', Krym (= Crimea), Ukraine, 1890, 1895(?), leg. A. E. Kessler; two males, ZIN 9249, 9250, skull, resp. skull and skin; vicinity of Simferopol', Krym (= Crimea), Ukraine, 1889, leg. A. E. Kessler; sex unknown, ZMMU S29157, skull; Doneck Distr., Ukraine, 31 August 1926, leg. Kalabukov; male, ZMMU S29432, skull; St. Tarasovka, Krasnodar Region, Russia, 17 Aug. 1925, leg. V. Raevskij, female, ZIN 62691, skull and dry skin; Malye Melešty near Kišiněv [= Meleşti near Chişinau]), galleries, Moldavia; 27 Jan. 1976, leg. E. Buntova; two males, one female, ZIN 55594–55596, skulls; districts of Tiraspol' and Orgeev, galleries, Moldavia; 24–27 Feb. 1969, leg. P. P. Strelkov.

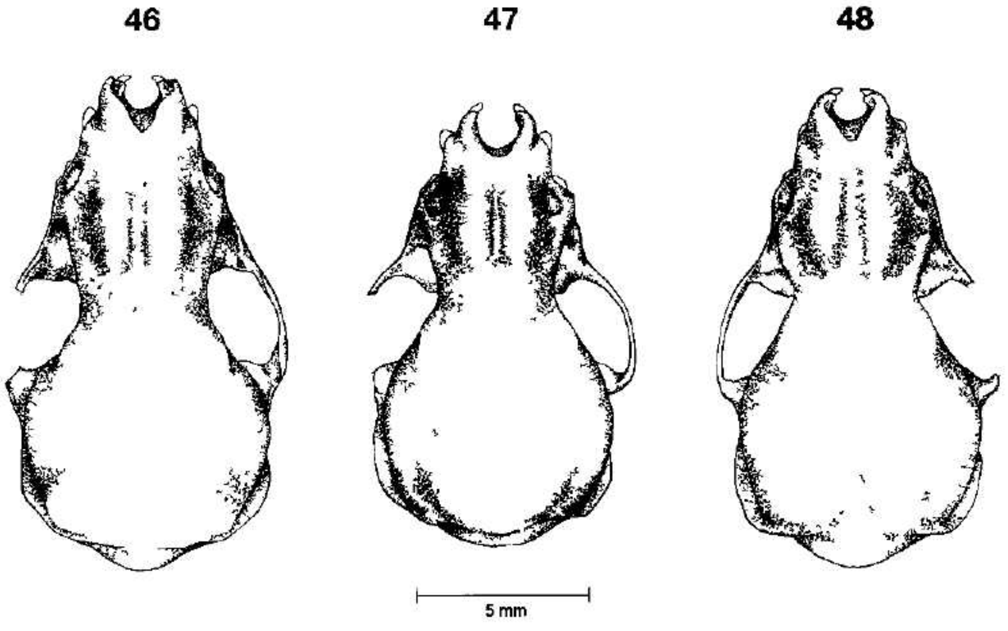
TYPE LOCALITY. Kurkužin [Куркужин] village, near Vladikavkaz in Northern Ossetia, northern slope of the Greater Caucasus Mts., Russia (Kusjakin 1935, Rossolimo & Pavlinov 1979). This site lays in the Kabardino-Balkarskaja Republic according to Strelkov (1983b).

DESCRIPTION. Large bat, almost of the size of *M. brandtii*; skull middle sized to large (LCr 13.3–14.9 mm), with frontal and occipital regions convex (Figs 48, 51, 80); upper canine middle long to long (mesiodistally, LCn 0.79–1.05 mm) and rather narrow, cingulum narrow oval to rhombic (RCn 1.12–1.50), crown has a rhombic basis with mesial, distal, palatal and labial edges, with a large and very distinct mesiodistal concavity and a smaller, but distinct labiodistal basal concavity, with a groove between the mesial and labial edges (Fig. 57); low cusp on the mesiopalatal edge of cingulum of P^4 present or absent (ACin 0.00–0.12 mm), premolar- and molar-row middle long (Figs 6, 7), P^3 and P_3 somewhat reduced, middle robust to small, P^3 mostly reaches $^1/_2$ of P^2, mostly located in the teeth-row (Fig. 57), sometimes displaced palatally; paraconules on molars always absent, metalophs absent in most cases, paralophs and metaconules well developed (Tab. 1, Fig. 63); I^2 with a shallow groove or a small protuberance of the palatal edge (Fig. 70). The whole penis is equally broad, but relatively broader than in *M. mystacinus* s. s. (Fig. 76), baculum middle-sized to large, rather narrow, with broad "wings", strong flexure in dorso-ventral direction and a massive basal part; the "head" is wide and "wings" are feebly marked and have no edging or very slender one (Figs 24–30). Colour of adults rather light, back brown to light brown or rusty, proximal parts of back hair dark brown, distal ends of back hair brown to rusty with golden or ochre hinge, belly distinctly bicoloured, proximal parts of hair dark grey to brown-grey, distal ends of hair ochre, cream-coloured to white, colours sharply divided on shoulders; hairless parts dark brown, basis of the ear and of tragus lighter brown (Figs 72, 73) Wing middle-sized to large (LAt 32 2–36 7 mm) Size and selected statistical parameters are listed in App III, Tabs 4, 7, 8

Taxonomic note This is probably the only taxon, in which characters clinally change in the known part of its range (see Distribution) In spite of that, all subpopulations probably belong to a single subspecies However, more data are needed from both the western part of the distribution area (i e Europe and the Middle East) and from Central Asia, especially from the steppe regions of Mongolia, and Tuva and Čita Regions of Siberia, Russia, where the bats continue to be referred to as *M mystacinus* s. l (sensu Strelkov 1983a) In addition, the population of Crete requires revision after more comparative material from this island is collected The specimen of *M aurascens* from Crete seem to be rather distinct – unfortunately it is just the only examined specimen from the island, which precludes any taxonomic interpretation of the record

Distribution Description of the distributional range of *Myotis aurascens* is a matter of future research, because the revised specimens do not cover its whole expected area In is clear, that the species occurs in south-eastern Europe, in the steppe belt of eastern Europe and in the Caucasus region

The westernmost record is available from Mt Altissimo di Nago in northern Italy (which is close to the Po lowland) The area continues at the Dalmatian shore, where this species is the only representative of the *M mystacinus* group In the Balkans the area includes whole territory of Bulgaria, Greece, and Macedonia From southern Serbia (Kosovo) the species is known only from Pec (Petrov 1967, Benda 1999) In the Balkans, *M aurascens* often occurs sympatrically with *M*



Figs 46–51 Skulls of bats of the *Myotis mystacinus* group from the Balkans (Bulgaria) 46 49 – *M brandtii* (ZMS No 120, male Mazata cave Hristo Danovo vill , Plovdiv Dist) 47, 50 – *M mystacinus* (NMP 48485, male, Ladenica cave, Gela vill Smoljan Dist), 48, 51 – *M aurascens* (ZMS No 92 male Rila Mts , Beli Iskar dam, Sofija Dist) Figs 46–48 Dorsal aspect

mystacinus (and also with *M. brandtii*), but is evidently more abundant – in the revised material in the ratio of ca. 3 : 1 (e. g. 20 : 7 in Gorna Breznica in Bulgaria, and 3 : 1 in Ormylia in Greece, and 65 : 28 in the whole Balkan sample, see App. II–III). The centre of the area probably lays in east European steppes from Moldavia, through Ukraine and Crimea to lower Volga river and western Kazakhstan. In this region, it is again the only representative of the species group, but at the borders it occurs sympatrically with *M. mystacinus* s. s. and *M. brandtii* (northwest Moldavia, region of middle flow of the Volga river) and with *M. nipalensis* (Emba river in western Kazakhstan). In Asia, this species is known from all parts of the Caucasus region, where it is sympatrical with other species from the species group. Known south-eastern border of this species' area is marked by records from the following two localities in the Caucasus region (see Fig. 45): Port Il'ič, Azerbaijan (cf. Strelkov 1983b) and Gutur-Su, NW Iran (cf. Harrison 1963).

It can be expected, that most bats from *M. mystacinus* s. l. in Turkey belong to this species (Helversen 1989a, Benda & Horáček 1998), especially in southern and south-western parts, where the occurrence of *M. mystacinus* s. s. or *M. nipalensis* is improbable for ecological and/or biogeographical reasons. This is supported by the records of Volleth (1987, 1989), who found in both Greece and Turkey karyotypically related forms ("*Myotis* sp. A"), different from *M. mystacinus* s. s. (we revised Greek material). The occurrence of *M. aurascens* in Asia Minor is supported also by the biometrical analysis presented by Albayrak (1991: 115). Geographically close Levantine records of *M. mystacinus* s. l. (Mt. Hermon and Golan Heights; Mendelssohn & Yom-Tov 1999) quite probably belong to *M. aurascens*.

***Myotis hajastanicus* Argyropulo, 1939 stat. n.**

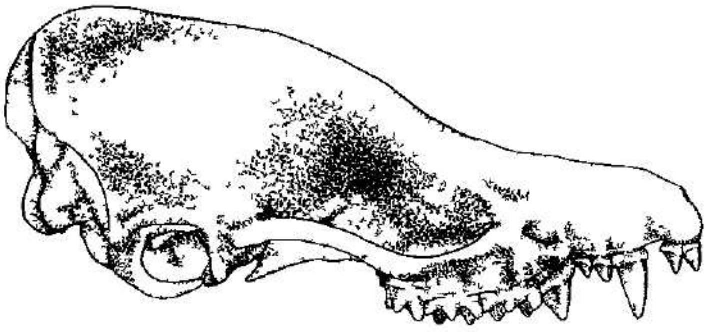
(Figs 58, 64, 70)

Myotis mystacinus hajastanicus Argyropulo, 1939: 27–29; Ellerman & Morrison-Scott 1951: 140; Hanák 1965: 362–366; Tsytsulina 1999: 65.
Myotis mystacinus mystacinus [partim]: Kuzjakin 1965: 96; Corbet 1978: 47; Koopman 1994: 103.
Myotis mystacinus auruscens [partim]: Strelkov 1983a: 263.

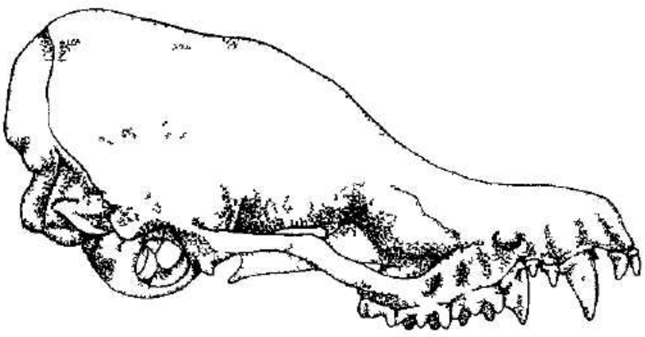
TYPE MATERIAL EXAMINED. **Paratypes**: two females, NMP 48536, 48537, skulls (mandibles omitted) and dry skins; *Šordža, eastern bank of the Sevan Lake, Armenia; 25 June 1928, leg. A. I. Argyropulo.*

TYPE LOCALITY. Šordža (= Nadeždino) [Шорджа (= Надеждино)], eastern bank of the Sevan Lake, 2000 m a. s. l., Armenia (Argyropulo 1939).
DESCRIPTION. Large bat, skull middle-sized to large (LCr 13.0–14.2 mm [M 13.66 mm]) with a rather flat frontal part and convex occipital part (Fig. 80); upper canine middle long (mesiodistally, LCn 0.78–0.91 mm [M 0.864 mm]) and very narrow, cingulum narrow oval (RCn 1.23–1.54 [M 1.388]), crown has a rhombic basis with distinct mesial, distal, palatal and labial edges with a large mesiodistal *and labiodistal concavities, a distinct groove between mesial and labial edge, and a shallow* groove between mesial and palatal edge (Fig. 58); P^4 always with a low cusp on the mesiopalatal edge of cingulum (ACin 0.02–0.11 mm), P^3 and P_3 small, P^3 less that $^1/_2$ of P^2 in height and located in the teeth-row (Fig. 58); paraconules on molars almost always absent, while paralophs, metalophs and metaconules are mostly developed (Tab. 1, Fig. 64). The teeth-row is in the relation to skull length extremelly short, in the absolute values shorter than in *M. mystacinus* s. s. (Fig. 44; P^2P^3 0.62–0.76 mm [M 0.683 mm], P_2P_3 0.67–0.86 mm [M 0.776 mm], M^1M^3 2.79–3.16 mm [M 2.932 mm], M^1M^3 3.16–3.37 mm [M 3.241 mm]); I^2 with a small protuberance on the palatal edge of cingulum, or – more often – cingulum has a smooth edge (Fig. 70). The structure of baculum is unknown (all examined specimens were females). Colour of adults light, back light brown, back hair long, proximal parts of back hair brown, distal ends of back hair ochre with yellowish or golden hinge, belly distinctly

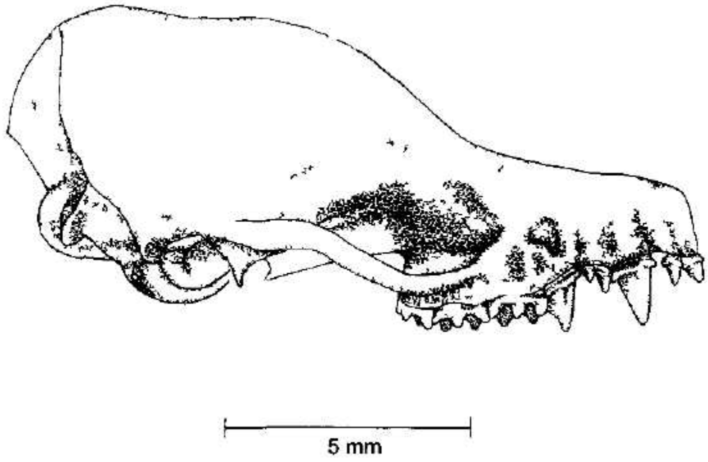
49



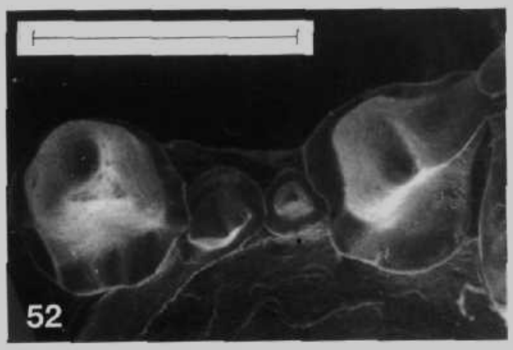
50

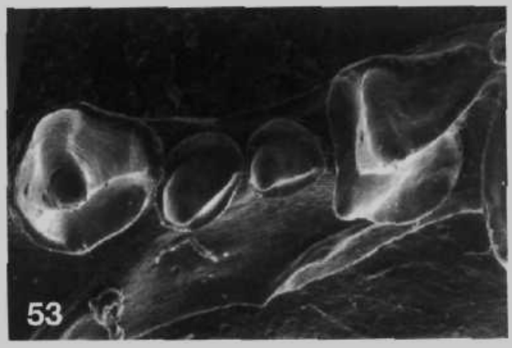


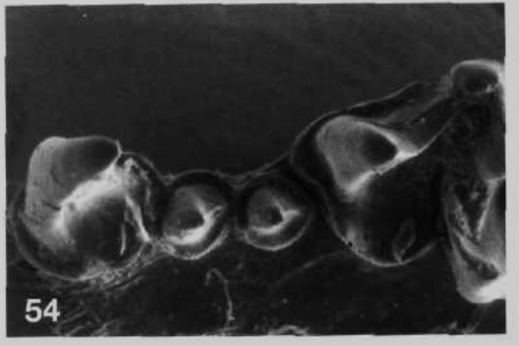
51

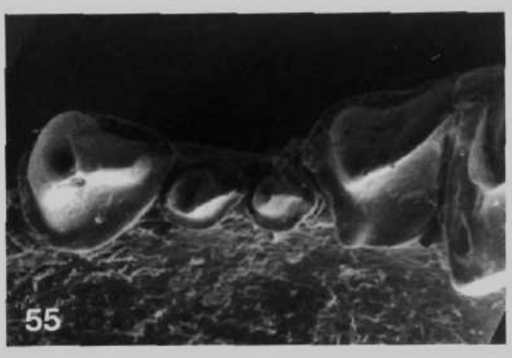


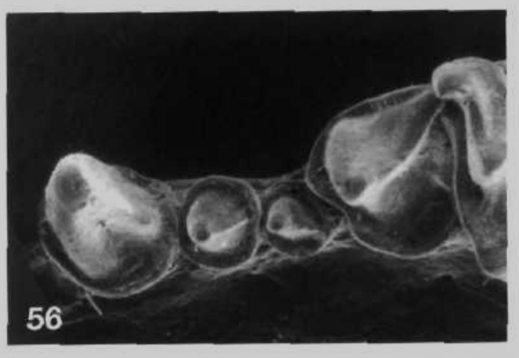
Figs 46 51 Skulls of bats of the *Myotis mystacinus* group from the Balkans (Bulgaria) Figs 49 51 Lateral aspect For explanation see p 363

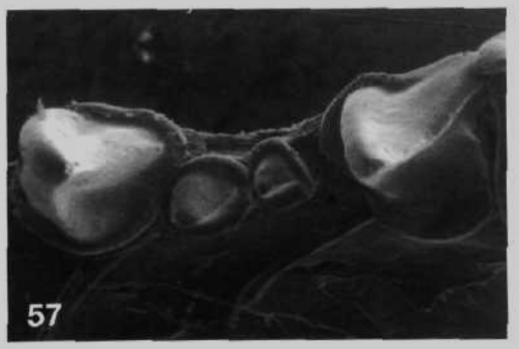

52

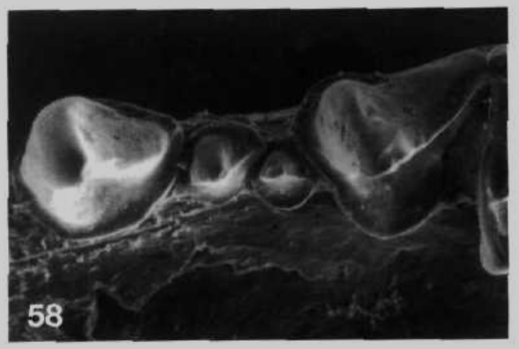

53

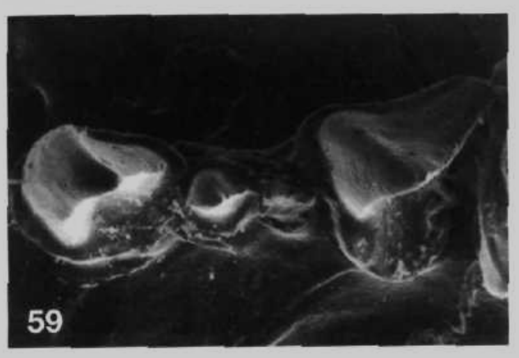

54


55


56


57


58


59

←

Figs 52–71 Dental characters in *Myotis mystacinus* group Specimens 52 – *M muricola*, SMO sa10, Sapulut, Borneo (Sabah, Malaysia), 53, 66 – *M brandtii*, ZMS No 120, Mazata cave (Plovdiv Dist), Bulgaria, 54, 62 – *M ikonnikovi*, NMP 48544, Svjatoj Nos isthmus, Burjatskaja Republic, Russia, 55, 60, 67 – *M mystacinus* s s , NMP 48485, Ladenica cave (Smoljan Dist), Bulgaria, 56, 61, 68 – *M mystacinus* s s , NMP 48504, Gorna Breznica (Blagoevgrad Dist), Bulgaria, 57, 63, 69 – *M aurascens*, ZMS No 92, Belt Iskar dam (Sofija Dist), Rila Mts , Bulgaria, 58, 64, 70 – *M hajastanicus*, NMP 48537, Šordža vill , Sevan Lake basin, Armenia, 59, 65, 71 – *M nipalensis*, NMP 48085, Sirbasan (Kars Dist), Turkey Figs 52–59 Canines and premolar-rows Scale 1 mm

bicoloured, proximal parts of belly hair brown, distal ends of belly hair creme-coloured to white, distinct boundary between colours on shoulders, hairless parts dark brown, basis of the ear and tragus less dark Wing large (LAt 34 5–37 3 mm [M 35.59 mm]), which corresponds with the high tail length, mentioned in the original description of this form by Argyropulo (1939: 29) Size and selected statistical parameters are given in App III, Tab. 5

DISTRIBUTION This form is known only from the Sevan Lake basin in Armenia (examined material originated from three localities, incl. Šordža, Čkalovka, and Basargečar) and its nearest surroundings (Aparan) (Fig 45)

Myotis nipalensis (Dobson, 1871) stat. n.

(Figs 23, 59, 65, 71, 74, 75)

Vespertilio nipalensis Dobson, 1871 214, Dobson 1876 141, Dobson 1878 302–303
Myotis meinertzhageni Thomas, 1926 609
Myotis mystacinus przewalskii Bobrinskoj, 1926 95, Bobrinskoj 1929 219, Allen 1938 217–218, Kuzjakin 1950 280, Ellerman & Morrison-Scott 1952 140, Abelencev et al 1956 341, Kuzjakin 1965 96, Strelkov 1983a 264, Koopman 1994 103, Kruskop & Borissenko 1996 331–335, Yongzu et al 1997 36–37, **syn. n.**
Myotis mystacinus transcaspicus Ogneff et Heptner, 1928* 260, Ognev 1928 453, Kusjakin 1935 431, Ellerman & Morrison-Scott 1952 140, Abelencev et al 1956 341, Misonne 1959 25, Koopman 1994 103, **syn. n.**
Myotis mystacinus transcaspica Ognev, 1927 [sic] Strelkov 1963 166
Myotis mystacinus kukunorensis Bobrinskoj, 1929 221, Abelencev et al 1956 341, **syn. n.**
Myotis mystacinus kukunoriensis [sic] Ellerman & Morrison-Scott 1952 140
Myotis mystacinus sogdianus Kuzjakin, 1934 321, Ellerman & Morrison-Scott 1952 140, Kuzjakin 1965 96, Koopman 1994 103, **syn. n.**
Myotis mystacinus pamirensis Kusjakin, 1935 431, Kuzjakin 1950 282, Ellerman & Morrison-Scott 1952 140, Abelencev et al 1956 341, Strelkov 1963 166, Kuzjakin 1965 96, **syn n.**
Myotis mystacinus nipalensis Ellerman & Morrison-Scott 1952 139, Corbet & Hill 1992 123, Hill 1983 154–155 Koopman 1994 103
Myotis mystacinus hajastanicus Hanak 1965 362–366, Albayrak 1991 118 [partim]
Myotis "mystacinus" przewalskii [partim] Stubbe & Chotolchu 1968 31–35
Myotis przewalskii [partim] Helversen 1989a 12–13
Myotis mystacinus meinertzhageni Corbet & Hill 1992 123

TYPE MATERIAL EXAMINED *Myotis meinertzhageni* Thomas, 1926 **holotype** female, BMNH 26 3 1 1 , skull and dry skin junction of Nubra and Shyok rivers, Ladak, Jammu and Kashmir, India *Myotis mystacinus przewalskii* Bobrinskoj, 1926 **holotype** sex unknown, ZIN 13906, skull and dry skin, Moldja river valley, Russkij hrebet [= Korian] range, Kashgaria, Eastern Turkestan, China, 4 May 1885, leg N M Prževalskij **Paratypes** (3) three ind of sex unknown, ZIN 13904, 13905, 13907, skulls and dry skins, the same locality as in holotype, 4 May 1885, leg N M Prževalskij *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928 **holotype** male, ZMMU S29214, skull and dry skin, Germad, Kopetdag Mts , Zakaspijskaja Oblast' [= Transcaspian Region] Turkmenistan, 12 June 1925, leg. S. I. Ognev. *Myotis mystacinus kukunorensis* Bobrinskoj, 1929: **holotype**: sex unknown, ZIN 2147, skull and dry skin, Belekut-gomi on Huang-He river, to south of the Kuku-Nor [= Qinghai Hu] Lake, Eastern Tibet, China, 18 May 1880, leg. N. M. Prževalskij. *Myotis mystacinus sogdianus* Kuzjakin, 1934: **holotype**: female, ZMMU S6819, skull, Taškent, Uzbekistan, 14 Sept. 1932, leg. A. P. Kuzjakin. *Myotis mystacinus pamirensis* Kusjakin, 1935: **holotype**: female, ZMMU S9265, skull; Jašil'-Kul' Lake, Pamir Mts., Tajikistan, 27 Aug. 1934, leg. R. N. Meklenburcev.

---

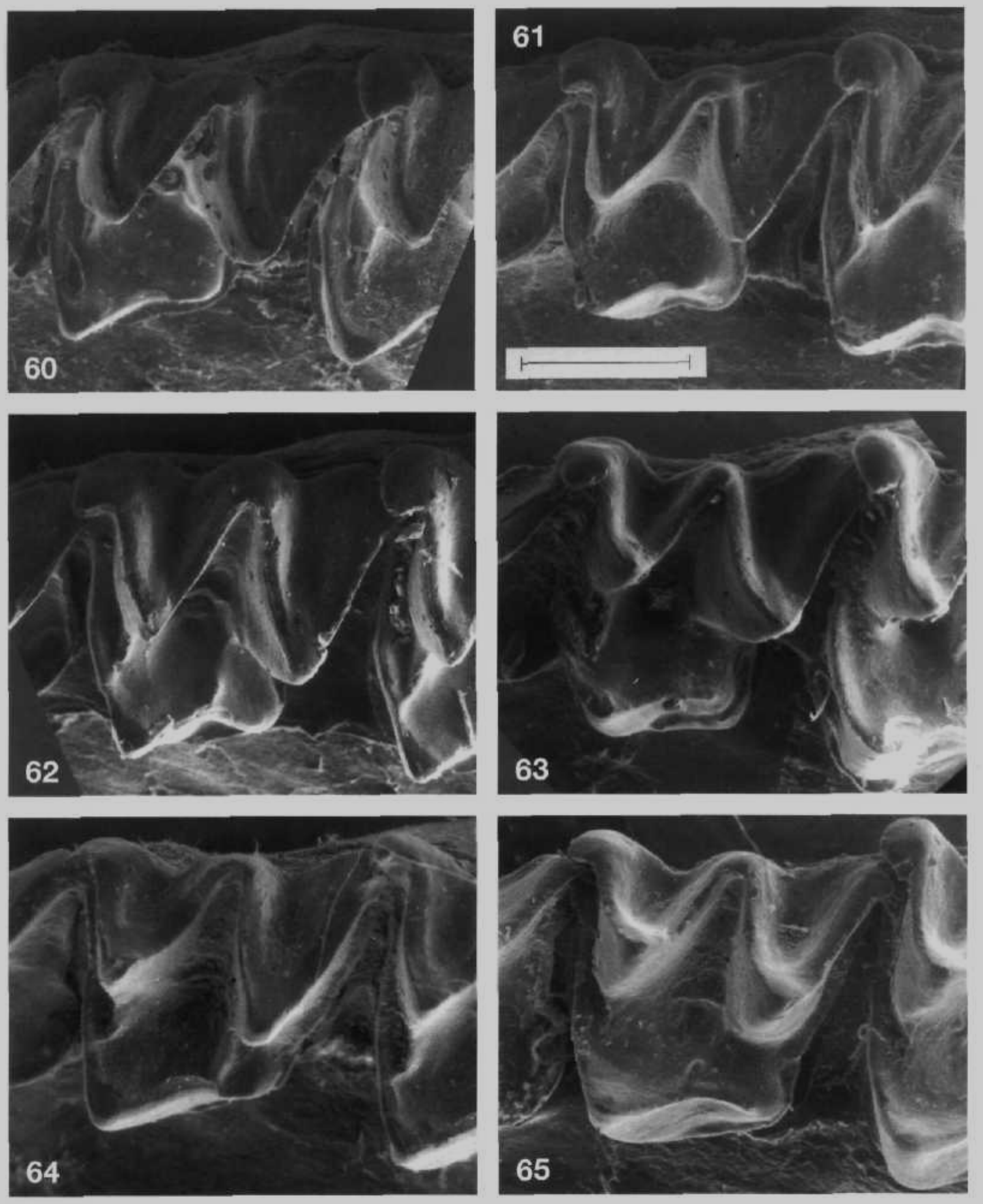
* *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928 is a senior synonym of *Myotis mystacinus transcaspicus* Ognev, 1928 The description of Ogneff & Heptner (1928) was issued in *Zoologischer Anzeiger* 75(11/12) on March 1, 1928 The description of Ognev (1928) is published as a book without exact date of issue, it is therefore necessary to consider the December 31, 1928 as the date of publication (see ICZN 1999)

TYPE LOCALITY. Kathmandu, Nepal (Dobson 1871).

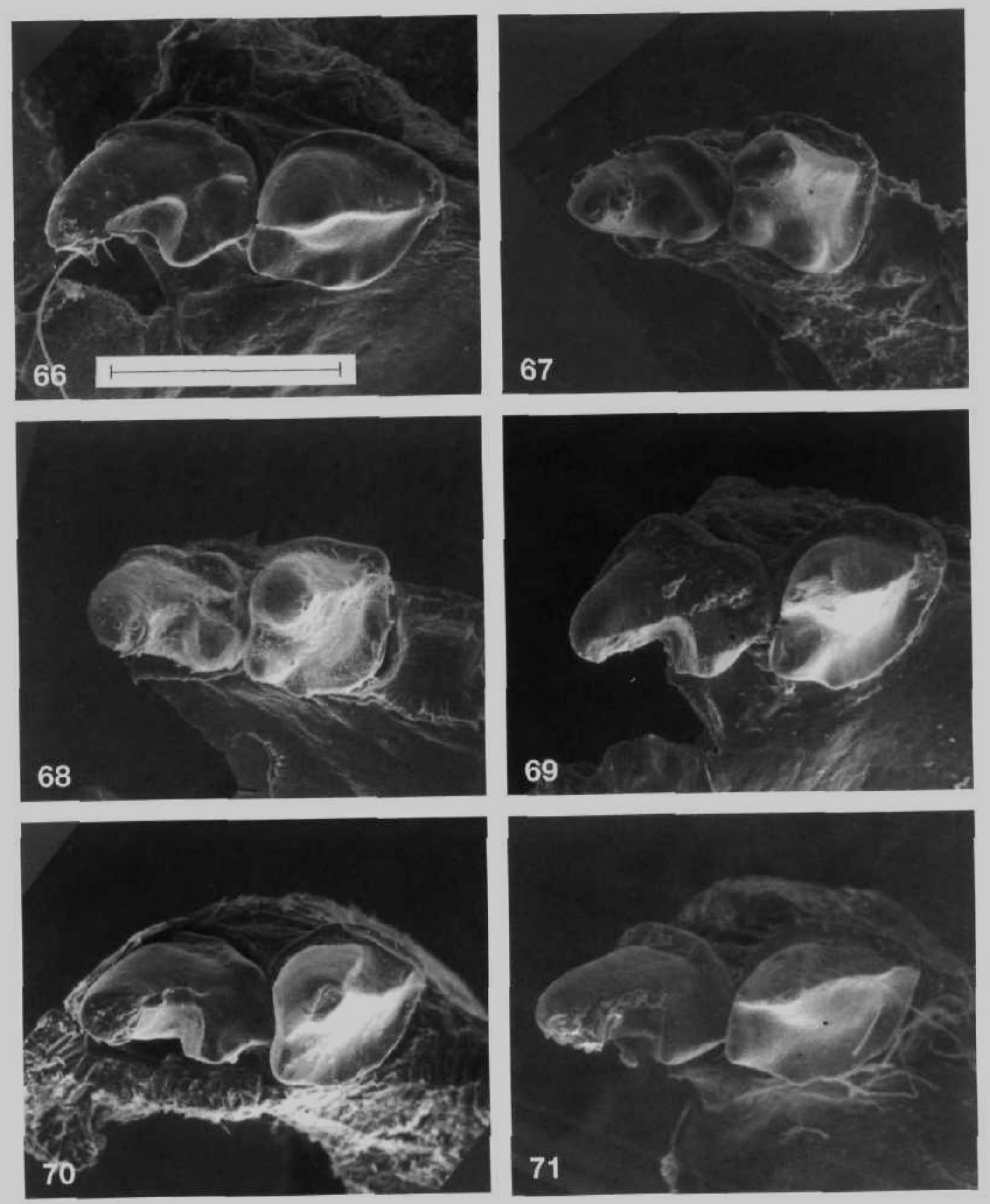
DESCRIPTION. Note: Dimensional characters are valid only for west Palearctic population, while qualitative characters are valid for the whole species. Middle-sized bat; skull small to middle-sized (LCr 12.7–13.9 mm) with less convex or flat frontal region and rather flat parietal part (Fig. 80); upper canine middle long (mesiodistally, LCn 0.83–0.96 mm) and narrow, cingulum narrow oval (RCn 1.25–1.51), crown has a rhombic basis with mesial, distal, palatal and labial edges, with large mesiodistal and labiodistal concavities, with a convex surface or a shallow groove between mesial and palatal edge (Fig. 59); P^4 with a low or middle high cusp on the mesiopalatal edge of cingulum, the cusp is exceptionally absent (ACin 0.00–0.18 mm), premolar-row very short to middle long, molar-row of the same length (Figs 6, 7), P^3 and P_3 small, P^3 small, reaching only $^1/_3$–$^1/_2$ of P^2 in height, *mostly located in the axis of the teeth-row (Fig. 59), but sometimes displaced palatally (Tab. 1)*; paraconules and metalophs on molars mostly absent, paralophs and metaconules mostly well developed (Tab. 1, Fig. 65); I^2 has a shallow groove or small protuberance on the palatal edge of cingulum (Fig. 72). Penis equally broad, baculum middle-sized, rather narrow, with a small "head", without great flexure in dorso-ventral direction, but with expressed "wings" with narrow edging (Fig. 23). Colour of adults rather light, back brown to light brown, proximal parts of back hair dark brown, distal ends of back hair rusty brown with ochre hinge, belly distinctly bicoloured, proximal parts of belly hair dark grey or brown, distal ends of belly hair ochre, creme-coloured to white, distinct colour boundary on shoulders (Figs 74, 75); hairless parts dark brown. Wing middle-sized to large *(LAt 32.2–37.3 mm). Size and selected statistical parameters are given in App. III, Tabs 6, 8, and for* the east Turkestan population in Tab. 11.

TAXONOMIC NOTE. *M. nipalensis* is a highly diversified form, as regards the above listed characters. Considering the large area (see Distribution), and especially because it inhabits a variety of biotopes from lowlands to high mountains, it is very probable, that several different a well recognizable populations do exist within this form, which could be given the subspecies rank. Sufficiently large samples from the whole area are necessary for the evaluation of the subspecific differentiation of this species. Available revisions (Hanák 1965, Strelkov 1983a, and our results) indicate, that the easternmost, mainly mountain population differs from the western, i. e. mainly desert populations (cf. App. III, Tabs 6 and 11). Hence, the oldest name applied to these bats from the western Palearctic can be probably used for the populations studied by us: *Myotis nipalensis transcaspicus* Ogneff et Heptner, 1928.

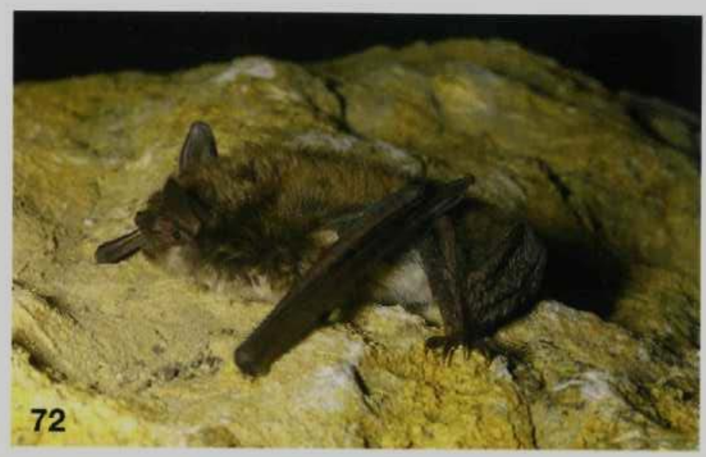
DISTRIBUTION. According to the restudy of the type material it seems probable, that this species occurs in a large part of the Asian area now believed to be inhabited by *M. mystacinus* s. l. (sensu Strelkov 1983b, Koopman 1994, Bates & Harrison 1997, Yongzu et al. 1997, etc.). The area includes Asia from the Caucasus Mts. and the Caspian Sea in the west to Eastern Turkestan and Tibet in the east, *including lowland deserts of Middle Asia (Karakum and Kyzylkum) and high mountains of* Middle and Central Asia (Hindukush, Himalayas, Kunlun Shan) with overlaps on upland plateaus. The southern border of the area is probably formed by southern slopes of Hindukush and of the Himalayas, the extreme south-eastern records are known from Meghalaya in eastern India (if the bats were not mistaken for another species, such as *M. muricola*); this part of the distribution range was described by Hill (1983) and Bates & Harrison (1997), respectively. The northern border is difficult to describe, but it probably follows the parallel 45° N (from Kazakhstan to Mongolia and

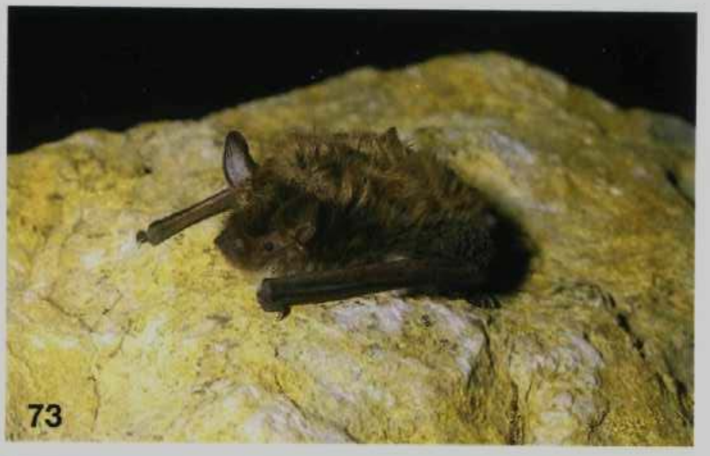


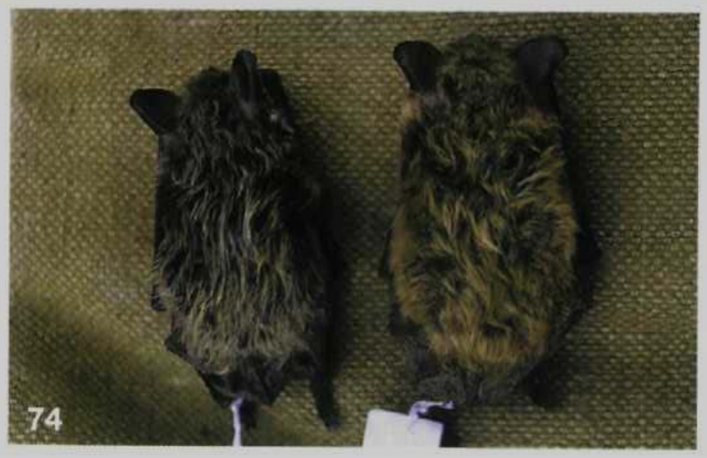
Figs 52–71. Continuation. Figs 60–65. Molar characters (M^1). For explanation see p. 367. Scale 0.5 mm.

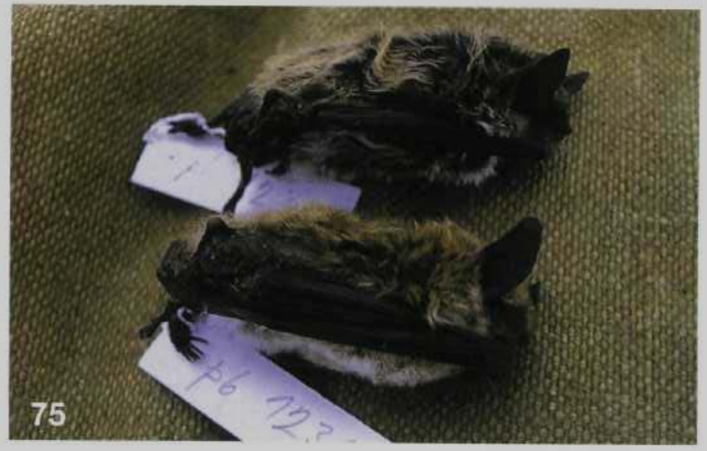


Figs 52–71. Continuation. Figs 66–71. Incisive characters (I^1–I^2). For explanation see p. 367. Scale 0.5 mm.

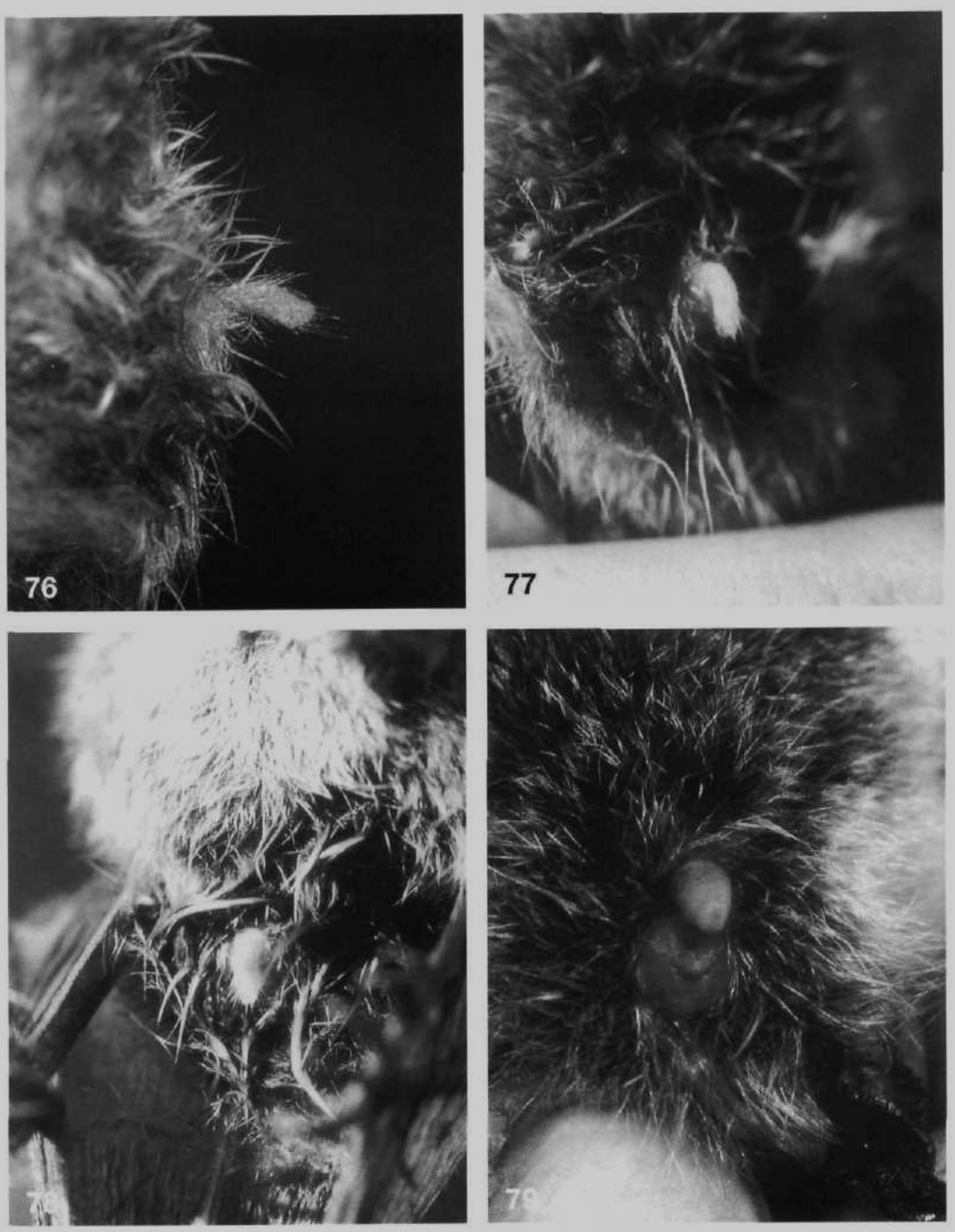

72


73


74


75

Figs 72–79. External characters of some species from *Myotis mystacinus* group. Figs 72, 73, 76. *M. aurascens*; Metamorfossi, Greece (26 Sept. 1988, leg. I. Horáček, photo by J. Červený). Figs 74, 75. *M. nipalensis*; males, Bastam, W-Azerbaijan Prov., Iran (29 Sept. 1998, leg. P. Benda, A. Reiter, M. Uhrin & M. Andreas, photo by A. Reiter). Figs 77, 78. *M. ikonnikovi*; Svjatoj Nos isthmus, Burjatskaja Republic, Russia (1991, leg. and photo by A. Reiter). Fig. 79. *M. brandtii* cf. *gracilis*; Svjatoj Nos isthmus, Burjatskaja Republic, Russia (1991, leg. and photo by A. Reiter). Figs 72–75. External habitae of the bats.



Figs 72–79. Continuation. 76–79. Shapes of penis. For explanations see p. 371.

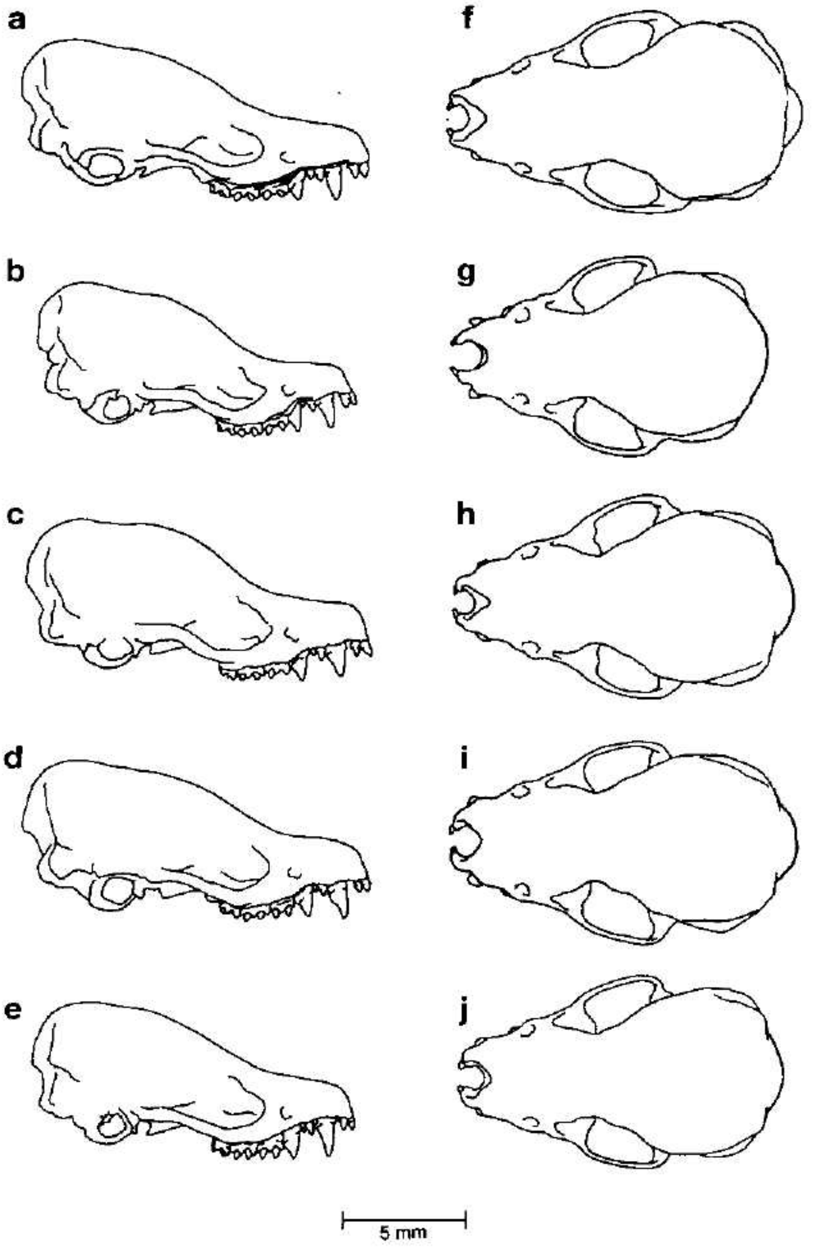


Fig. 80. A comparison of dorsal and lateral contours of skull of five taxa from the *Myotis mystacinus* group (schematic after real skulls, comp. Figs 46–51) commig from the western Palearctic. a, f – *M. brandtii*; b, g – *M. mystacinus mystacinus*; c, h – *M. aurascens*; d, i – *M. hajastanicus*; e, j – *M. nipalensis transcaspicus*.

southern Siberia), where it can be sympatric with *M. aurascens* (see common records on the Emba river), so that the bats can be misidentified and belong to the latter species (which is probable from the ecological point of view). *Hence, the region should be re-evaluated from this point of view.*

In the western Palearctic, *M. nipalensis* is known from the Caucasus region, where it occurs sympatrically with *M. aurascens*, *M. hajastanicus*, and *M. mystacinus* s. s., the former two of which belong to the *nipalensis* subgroup (Fig. 45), and from the western Kazakhstan, where it is sympatric at least with *M. aurascens*. The westernmost records are known from NW Turkey (Sirbasan, Van, cf. Benda & Horáček 1998) and NW Iran (Bastam, cf. Benda et al. 1999, see Figs 74, 75).

Notes to north-eastern Palearctic taxa

Myotis brandtii gracilis Ognev, 1927

(Fig. 79)

Myotis mystacinus gracilis Ognev, 1927: 145; Ognev 1928: 454; Kusjakin 1935: 431; Abelencev et al. 1956: 341; Hanák 1965: 363.
Myotis mystacinus mystacinus: Kuzjakin 1950: 279; Kuzjakin 1965: 96; Corbet 1978: 47.
Myotis mystacinus gracilus [sic]: Strelkov 1963: 166.
Myotis brandtii gracilis: Strelkov 1983a: 259; Tiunov 1984: 85; Koopman 1994: 103; Kruskop & Borissenko 1996: 331–335; Tiunov 1997: 36; Kruskop 1998: 103.
Myotis gracilis: Yoon & Son 1989: 383; Yoshiyuki 1989: 99; Horáček et al. in press.

TYPE MATERIAL EXAMINED. **Lectotype** (by present designation): female, ZMMU S104423, skull (skin destroyed); Vladivostok, Russia; leg. N. P. Krylov. The specimen is one from two syntype specimens of Ognev's (1927) description, the second was destroyed (A. V. Borissenko and S. V. Kruskop, ZMMU, in verb.).

TYPE LOCALITY. Near Vladivostok [Primorskij Region, Russia] (Ognev 1927).
COMMENTS. Strelkov (1983a) observed, that this form exhibits all indentification characters of the species *M. brandtii*. His result is confirmed by our examination of the type specimen. Strelkov (1983a) showed that this population differs from the nominotypic one in being smaller, which led him to separate the Far East population at the subspecies level. Tiunov (1997) demostrated, that southern and northern populations of *M. brandtii* differ metrically in the Far East, and expressed these observations taxonomically, attributing smaller individuals of the southern population from mixed forests to *M. b. gracilis* (Primorskij Kraj Region, southern Habarovsk Region, Japan), and larger individuals of the northern population from coniferous forests to *M. b. brandtii* (northern Habarovsk Region, Kamchatka, Magadan Region). Horáček et al. (in press) tentatively solved this situation by recognition of *M. gracilis* as a separate species (see also Yoshiyuki 1989).

It is confirmed on the basis of published revisions (Fedorov 1978, Strelkov 1983a, Tiunov 1997, our results), that the species *M. brandtii* occurs in the eastern margin of the Palearctic. It is necessary, however, to evaluate the taxonomic status of these populations: (1) If clinal variation in metrical characters occurs on the south-north gradient, then the two populations need not be separated taxonomically (as in the west Palearctic population). (2) If abrupt shift in metrical characters between the southern and the northern populations is present, then it should be expressed taxonomically (see Tiunov 1997). (3) If two distinct populations of larger and smaller individuals exist in the region, then they should be separated at the species level (see Yoshiyuki 1989, Horáček et al. in press). Anyhow, until a detailed reconsideration of the topic, we prefer Strelkov's (1983a) opinion, the only one which resulted from a large scale revision of the material covering almost the whole range of *M. brandtii*. This conclusion is supported also by the results of Kruskop (1998).
DISTRIBUTION. Eastern part of the species range: eastern Siberia to the Baikal Lake in the west, Kamchatka, Amur Region, Korea, Sakhalin, Hokkaido (Ognev 1927, Strelkov 1983a, Yoshiyuki 1989, Won & Smith 1999). Tiunov (1997) restricted the distribution range of this form in Russia to

the southern part of the Russian Far East, approximately south of the Uda river (incl. the islands of Sakhalin and Kunashir).

Myotis ikonnikovi Ognev, 1911

(Figs 18, 54, 62, 77, 78)

Myotis ikonnikovi Ognev, 1911: 477; Ognev 1927: 145; Ognev 1928: 455; Ellermann & Morrison-Scott 1951: 141; Kusjakin 1935: 431, Strelkov 1963: 166, Hanák 1965: 353–366; Corbet 1978: 48; Tiunov 1984: 85, Pavlinov & Rossolimo 1987: 37; Yoshiyuki 1989: 92, Koopman 1993: 211, Yoshiyuki 1993: 135, Koopman 1994: 103, Pavlinov et al. 1995: 99; Kruskop & Borissenko 1996: 332–333; Tiunov 1997: 37; Yongzu et al 1997: 37–38; Kruskop 1998: 101–103; Pavlinov & Rossolimo 1998: 23; Won & Smith 1999: 13; etc
Myotis mystacinus ikonnikovi: Bianchi 1917: 80
Myotis muricola ikonnikovi: Kuzjakin 1950: 272, Kuzjakin 1965: 96
Myotis mystacinus: Fedorov 1978: 1281

TYPE MATERIAL EXAMINED. **Lectotype**: female, ZMMU S96372, skull and dry skin; Evseevka village, 27 versts SE Hanka Lake, Imanskij Uezd Dist., Primorskij Kraj Reg., Russia; 2 June 1910, leg. N. F. Ikonnikov, designed by Rossolimo & Pavlinov (1979: 12). **Paralectotype**: female, ZIN 8997, alcohol specimen (skull not extracted); the same locality as lectotype, 2 June 1910, leg. N. I. Šingarev, identified as a paralectotype by Baranova et al. (1981: 13). No other paralectotypes are known.

TYPE LOCALITY. Evseevka [Евсеевка] village, Imanskij Uezd Dist., Primorskaja Oblast' Reg. [= Primorskij Kraj Reg.], Russia (Ognev 1911).

COMMENTS. The validity of this species will be evidenced and confirmed elsewhere Tsytsulina (in press). Here we will just stress, that Kuzjakin's (1950, 1965) opinion that *ikonnikovi* is conspecific with *Myotis muricola* (Gray, 1846) or the opinion that the two species belong to a single group or subgroup (Corbet 1978, Koopmann 1994) is not substantiated. According to dimensional characters and proportions of skull, and especially according to dental characters (cf. Figs 52, 54, 62, see also Godawa Stodmark 1998) and penial characters (cf. Figs 18, 77, 78), *M. ikonnikovi* is closely related to *M. m. mystacinus*. This conclusion has supported also by results of dental comparations of Godawa Stormark (1998) and baculum studies of Strelkov (1989).

DISTRIBUTION. *M. ikonnikovi* is distributed in the zone of the east Palearctic mixed forests and light taiga from the Altai Mts (Kazakhstan and Russia) through Mongolia, southern Siberia, Manchuria and the Far East to Hokkaido (Strelkov & Šajmardanov 1983, Švecov et al. 1984, Yoshiyuki 1989, 1993, Tiunov 1997, Yongzu et al. 1997, Botvinkin 1999, Won & Smith 1999, etc.). Hence, it is the vicariant form of the west Palearctic *M. mystacinus* s. s.

DISCUSSION

Our study confirmed the specific status of *M. brandtii* and *M. ikonnikovi*. In the western Palearctic, *M. brandtii* does not form morphologically distinct populations according to our data. This agrees with Strelkov (1983a), who assigned all bats of this species from the western Palearctic to the subspecies *M. brandtii brandtii*. Some metrical characters form west-east or south-north gradients, respectively, which corresponds with the Bergmann's rule (Bergmann 1847), which was also found in the ecologically similar bat, *Myotis daubentonii* (Kuhl, 1817), by Bogdanowicz (1990).

The occurrence of *M. ikonnikovi* in the western Palearctic was not confirmed. Small individuals of *M. mystacinus* s. l., which were assigned to *ikonnikovi* are in fact smallest individuals of *M. mystacinus* s. s. This confirmed the expectation by Hanák (1965), and contradicts the opinion of Helversen (1989b).

Within *M. mystacinus* s. l., as understood e. g. by Strelkov (1983a, b) and Koopman (1993, 1994), four species were distinguished on the basis of a number of morphological characters and geographic distribution (sympatric occurrence), incl. *M. mystacinus* s. s., *M. aurascens*, *M. hajastanicus* and *M. nipalensis*. The first one corresponds with the forest or northern populations, while the latter three – formerly identified as "*prezewalskii*-Gruppe" by Stubbe & Chotolchu (1968) – belong to southern populations, known especially from steppe and/or desert areas. Within *M. mystacinus* s. s., three morphologically and geographically well defined subspecies were recognized, of which two were newly described. *M. hajastanicus* inhabits only a limited area, and is apparently monotypic. It is probably a relict population. An endemic species of the genus *Myotis* is already known from the Caucasus region: *Myotis schaubi* Kormos, 1935 occurs only in the eastern Armenia and western Zagros (Horáček & Hanák 1984, Benda et al. 1999). *M. nipalensis* is an Asian form, which enters the area of our interest only marginally. As mentioned above, at least three morphologically and geographically well defined subspecies probably exist within this species, but their status can be reconsidered only after through study of the populations from Kazakhstan, Middle and Central Asia (incl. China), and northern India. A review of the systematics was presented and the differences between *M. nipalensis* (understood as *M. mystacinus* s. l.) and bats of the *M. muricola* subgroup in northern India were described by Hill (1983); his conclusions agree with our results as regards pelage coloration.

The phenotypical distinctness of the westernmost "southern" form of *M. mystacinus* s. l., i. e. *M. aurascens*, was recognized earlier on the basis of the morphology of baculum and metrical characters (Strelkov & Buntova 1982, Strelkov 1989), and Strelkov (1983a) described it as a separate subspecies *M. m. popovi*. Helversen (1989a, b) recognized on the basis of karyological and genetic studies (Volleth 1987, 1989, Nemeth 1993) a valid species in the eastern Mediterranean, incorrectly calling it – solely on the basis of the data by Stubbe & Chotolchu (1968) – *M. przewalskii*. *M. aurascens* reaches south-eastern parts of Europe, from Ukraine, through the Balkans till northern Italy (Fig. 81). It is probable, however, that further study of museum specimens and/or field studies will result in the discovery of other localities, particularly in other parts of Italy, and along the Adriatic coast in Slovenia, Croatia, Montenegro, and Albania. Borders of the known distribution of *M. aurascens* corresponds with the July isotherm 20–25 °C, and with the area, where the period with a mean temperature over 20 °C lasts for ca. 2–3.5 months. Accordingly, not only the whole Italy, but also Pannonia could belong to the area of this species*. The restudy of the type material of *M. mystacinus mongolicus* Kruskop et Borissenko, 1996 indicates, that this steppe form could belong to *M. aurascens*. In morphological characters, *mongolicus* agrees more closeely with *M. aurascens* than with *M. nipalensis*. The differences between *M. m. mongolicus* and *M. nipalensis* (= *M. m. przewalskii*) were stressed already by Kruskop & Borissenko (1996). *M. aurascens* could be distributed in the steppe zone from Europe to the Central Asia. It is highly probable, that *M. aurascens* is much more distributed than indicated by the material examined (see App. II).

Worth mentionig is that the distribution of species as understand here closely correspond with the limits of major ecozones of the western Palearctic as delimited by Schultz (1995) and applied to the chiropteran biogeography by Horáček et al. (in press). The boreal zone (i. e. zone of northern coniferous forests) of the Palearctic is inhabited by *M. brandtii*. Temperate humid zone (i. e. zone of mixed forests) is inhabited by *M. mystacinus* s. s. (western Palearctic), *M. hajastanicus* (Armenia), and *M. ikonnikovi* (eastern Palearctic). Zone of Mediterranean subtropics are inhabited by *M. m occidentalis* ssp. n. (western Mediterranaen) and *M. aurascens* (eastern Mediterranean = zone of sympatry with other bats of the group). The temperate arid zone (i. e. Palearctic eremial zone) is inhabited by *M. aurascens* (steppe part = zone of allopatry in the species) and *M.* (*?aurascens*) *mongolicus* (Central Asian steppes); desert part of this zone (Middle Asian deserts) plus mountains and mountain plateaus of Central Asia are inhabited by *M. nipalensis*.

---

* Possible occurrence of *M. aurascens* in Pannonia is indicated also by a record of *Basilia mongolensis* Theodor, 1966 (Insecta: Diptera: Nycteribiidae) from Austria (Kock 1984). This parasite is probably limited to *M. mystacinus* s. l., or directly to *M. aurascens* in occurrence, being known from six localities in Central Asia and from six localities in the western Palearctic (Hůrka 1972, 1984, Hasbenli 1997). In addition to Austria, *Basilia mongolensis nudior* Hůrka, 1972 (western subspecies of *B. mongolensis*) was found in Greece, Bulgaria, and two-times in Asia Minor on *M. mystacinus* s. l., and one-times in Dalmatia on *Plecotus austriacus* (Fischer, 1829) (see Fig. 81). Host bats from Bulgaria (Gorna Breznica, Blagoevgrad Dist., two females, NMP 48509, 48510) was revised by us, and assigned to *M. aurascens*.

Another problem, which requires solution with respect to the nomenclature of the *M. mystacinus* group, is the taxonomic position of *Vespertilio Davidii* Peters, 1869 (type locality: Beijing, China). Peters (1869: 402–403) described this species as a form closely related to *M. mystacinus* (i. e. *M. mystacinus* group), from which it was said to differ in imperfectly described characters of the molariform dentition. This taxon was traditionally accepted as a valid species (Dobson 1876, 1878, Allen 1938, Ellermann & Morrison-Scott 1951, Yongzu et al. 1997, Horáček et al. in press). Dobson (1878: 300) placed it in the neighbourhood of *M. daubentonii*. Allen (1938) compared it with both

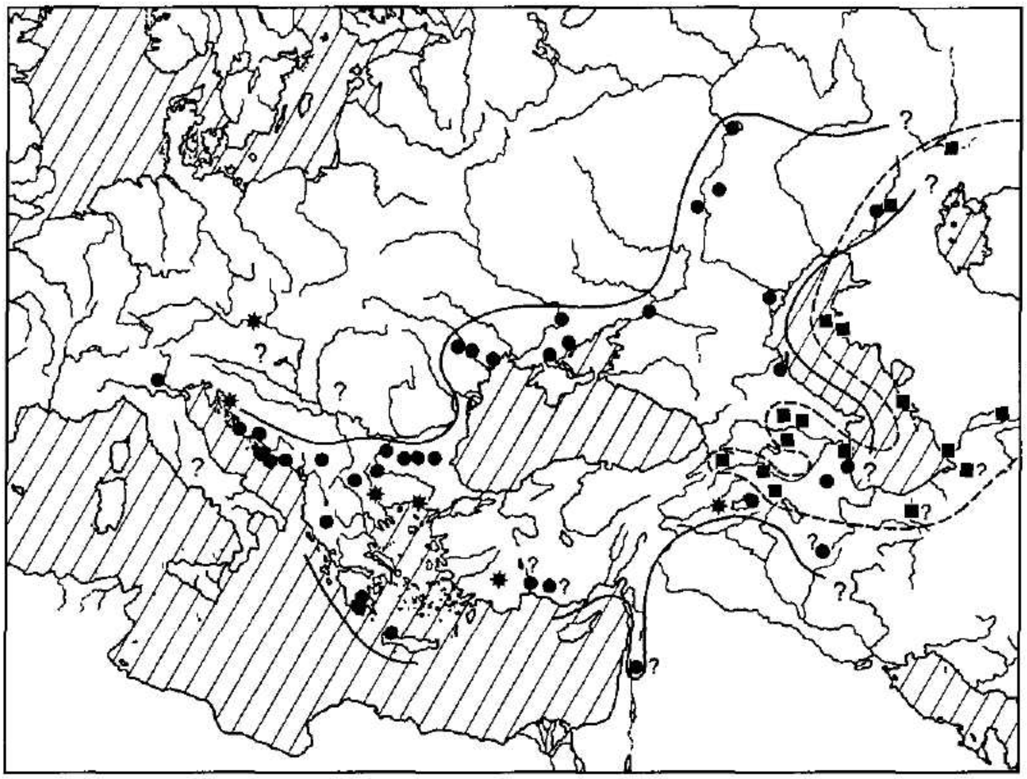


Fig 81. Approximate distribution of two newly defined species from the *Myotis mystacinus* group in the western Palearctic. Dots – marginal records of *M. aurascens*, squares – marginal records of *M. nipalensis*, asterisks – known records of *Basilia mongolensis nudior* (see text); solid line – expected border of distributional range of *M. aurascens*, dashed line – expected border of distributional range of *M. nipalensis*; question marks denote unknown continuation of the distribution range of *M. aurascens* (the larger ones) and the non-revised or not sufficiently revised material (the lesser ones)

M daubentonii and *M mystacinus* Tate (1941 551) and Ellermann & Morrison-Scott (1951 149) included it in the subgenus *Leconoe* Boie, 1830 Corbet (1978 47) tentatively (on the basis of Findley 1972, who included it in the *M mystacinus* group) and Koopmann (1993 213, 1994 103) included the taxon in *M mystacinus* as a subspecies *M mystacinus davidii* (Peters, 1869)

Although no morphological revision of this form has been done yet, its taxonomic validity has never been doubted, and the form was recognized either at the species or subspecies level *Vespertilio Davidii* is the oldest name applied to an Asian bat, which could have a relation to the *M mystacinus* group, so that the revision of the species could result in nomenclatural changes The only useful information presented by Peters (1869) is the forearm length (LAt), which is 31 5 mm in the holotype Taking into account the type locality, *V Davidii* could be a senior synonym of one of the following three taxa known from the temperate zone of the eastern Asia, i e *gracilis*, *ikonnikovi* and *nipalensis* Also, it can be a valid species, which can belong to the *mystacinus* or some other species group within the genus *Myotis*

Acknowledgements

The following persons kindly allowed us to use specimens under their care and for supplying additional information Manfred Ade (Zoological Museum, Humboldt University, Berlin), Uwe Fritz (Zoological Museum Dresden), Otto von Helversen (Erlangen), Vladimir Hanak and Ivan Horaček (Charles University, Prague), Carlos Ibañez (Biological Station Doñana), Theodora Ivanova (Zoological Museum Sofia), Paula D Jenkins (Natural History Museum, London), Darko Kovačic (Zoological Institute of Zagreb), Boris Kryštufek (Slovenian Natural History Museum, Ljubljana), Dieter Kock and Gerhard Storch (Senckenberg Museum, Frankfurt am Main), Igor Ja Pavlinov (Zoological Museum, Moscow State University), Manuel Ruedi (Natural History Museum, Geneve), Friederike Spitzenberger and Barbara Herzig (Natural History Museum, Vienna), Petr P Strelkov (Zoological Institute, St Petersburg), and Yoram Yom-Tov (Tel Aviv University)

For fruitful discussions and help with the evaluation of the material we are obliged to the following colleagues and friends Jaroslav Červeny, Vladimir Hanak, Ivan Horaček, Karel Hůrka, Jiři Mlikovsky, David Storch, Vladimir Vohralik, Jan Zima (Prague) Aleksej V Borissenko and Sergej V Kruskop (Moscow), Petr P Strelkov (St Petersburg), Boris Kryštufek (Ljubljana), Manuel Ruedi (Genève), Dieter Kock and Gerhard Storch (Frankfurt am Main) For photographs we are obliged to Jaroslav Červeny (Prague) and Antonin Reiter (Znojmo)

Ivo Klepáček (Institute of Anatomy, 1st Medical Faculty, Charles University, Prague) kindly allowed us to use the electron microscope in his institution This study was conducted with the support of a grant of the Ministry of Education of the Czech Republic No VS 97102, and grants of the Ministry of Culture of the Czech Republic Nos VZ F02/98 NMPM00001 and RK99P03OMG037

REFERENCES

ABELENCEV V I 1950 [On the bats of Transcarpathian Region and other western regions of the USSR] *Trudy Zool Muz Kiiv Derž Univ im T G Ševčenka* **2** 59–74 (in Russian)

ABELENCEV V I, PIDOPLIČKO I G & POPOV B M 1956 *Fauna Ukraini Tom I Ssavci Vipusk I [Fauna of Ukraine Part I Mammals Volume I]* Kiiv Vidavnictvo Akad Nauk Ukrainskoi RSR, 448 pp (in Ukrainian)

ALBAYRAK I 1991 Studies on Myotis mystacinus and Myotis brandti (Mammalia, Chiroptera) in Turkey *Mammalia* **55** 113–120

ALLEN G M 1938 *The Mammals of China and Mongolia Natural History of Central Asia Vol XI, Part I* New York The American Museum of Natural History, 620 pp

ARGYROPULO A I 1939 Uber einige Saugetiere Armeniens *Zool Sbornik* 1 (*Trudy Biol Inst* 3) 26–66 (in Russian, German summ)

ATANASSOV N & PESCHEV Z 1963 Die Saugetiere Bulgariens *Saugetierk Mitt* **11** 101–112

AULAGNIER S & DESTRE R 1985 Introduction à l'etude des chiroptères du Tafilalt (sud-est marocain) *Mammalia* **49** 329–337

BAAGØE H J 1973 Taxonomy of two sibling species of bats in Scandinavia Myotis mystacinus and Myotis brandtii (Chiroptera) *Vidensk Meddr Dansk Naturhistor Foren* **136** 191–216

BARANOVA G I, GUREEV A A & STRELKOV P P 1981 *Katalog tipovyh èkzempljarov kollekcii Zoologičeskogo Instituta AN SSSR Mlekopitajuščie (Mammalia) Vypusk I Nasekomojadnye (Insectivora), rukokrylye (Chiroptera), zajceobraznye (Lagomorpha) [Catalogue of type specimens in the collection of the Zoological*

Institute AN SSSR Mammals (Mammalia) Volume 1 Insectivores (Insectivora), bats (Chiroptera), lagomorphs (Lagomorpha)] Leningrad Nauka, 24 pp (in Russian)

Bates P J J & Harrison D L 1997 *Bats of the Indian Subcontinent* Sevenoaks Harrison Zoological Museum, 258 pp

Baud F 1977 Catalogue des types de mammifères et d'oiseaux du Museum d'Histoire naturelle de Geneve *Rev Suisse Zool* **84** 201–220

Benda P 1999 Three notes on the taxonomy of Myotis brandtii (Chiroptera Vespertilionidae) and on the history of its recognition in the western part of Europe *Lynx, n s* **30** 5–26 (in Czech, English summ)

Benda P & Horáček I 1995 Biometrics of Myotis myotis and Myotis blythi *Myotis* **32–33** 45–55

Benda P & Horáček I 1998 Bats (Mammalia Chiroptera) of the Eastern Mediterranean Part I Review of distribution and taxonomy of bats in Turkey *Acta Soc Zool Bohem* **62** 255–313

Benda P, Obuch J, Andreas M, Reiter A & Uhrin M 1999 New records of bats from Iran Pp 6–7 In Cruz M & Kazakiewicz K (eds) *VIIIth European Bat Research Symposium Abstracts* Krakow CIC and IASE PAS 88 pp

Bergmann C 1847 Uber die Verhaltnisse der Warmeokonomie der Thiere zu ihre Grosse *Gottinger Studies* **1** 595–708

Beron P 1961 Contribution a la connaisance des chauves-souris Bulgares *Fragm Balcan Mus Maced Sci Natur, Skopje* **3**(24) 189–195

Bianchi V 1917 Notes preliminaires sur les chauvesouries ou Chiropteres de la Russie *Ann Mus Zool Acad Sci St-Petersb* **21** 73–82 (in Russian, French title)

Bobrinskoj N A 1926 Note preliminaire sur les Chiropteres de l'Asie Centrale *Compt Rend Acad Sci URSS* **1926** 95–98 (in Russian, French title)

Bobrinskoj N 1929 Bats of Central Asia *Annu Mus Zool Acad Sci URSS* **1929** 217 244

Bogdanowicz W 1990 Geographic variation and taxonomy of Daubenton's bat, Myotis daubentoni, in Europe *J Mamm* **71** 205–218

Bogdanowicz W 1992 Sexual dimorphism in size of the skull in European Myotis daubentoni (Mammalia Chiroptera) Pp 17–25 In Horáček I & Vohralík V (eds) *Prague Studies in Mammalogy* Praha Charles Univ Press 246 pp

Botvinkin A D 1999 Ikonnikov's bat in Baikal area (distribution, relative abundance, roost sites, behaviour) *Plecotus et al* **2** 108–116 (in Russian, English summ)

Buša I K 1980 [Present status and history of research of bats in Latvia] Pp 106–114 In Kuzjakin A P & Panjutin K K (eds) *Voprosy teriologii Rukokrylye (Chiroptera)* [*Questions in Theriology Bats (Chiroptera)*] Moskva Nauka, 320 pp (in Russian)

Corbet G B 1978 *The Mammals of the Palearctic Region a taxonomic review* London and Ithaca British Museum (Natural History) and Cornell University Press, 314 pp

Corbet G B & Hill J E 1992 *The Mammals of the Indomalayan Region a systematic review* London British Museum (Natural History) 488 pp

DeBlase A F 1980 The bats of Iran Systematics, distribution, ecology *Fieldiana Zool, N S* **4** 1–424

Dobson G E 1871 Notes on nine species of Indian and Indo-Chinese Vespertilionidae, with remarks on the synonymy and classification of some other species of the same family *Proc Asiat Soc Bengal* **40** 210–215

Dobson G E 1876 *Monograph of the Asiatic Chiroptera and Catalogue of the species of bats in the Collection of The Indian Museum, Calcutta* Calcutta Indian Museum

Dobson G E 1878 *Catalogue of the Chiroptera in the Collection of the British Museum* London Order of the Trustees [of British Museum], 568 pp

Dulić B & Tortić M 1968 Verzeichnis der Saugetiere Jugoslawiens *Saugetierk Mitt* **8** 1–12

Dumitrescu M, Tanasachi J & Orghidan T 1963 La repartition des Chiropteres en Roumanie *Lucrarile Inst Speol "Emil Rakoviţa"* **1–2** 509–575 (in Romanian, French summ)

Egsback W, Kirk K & Roer H 1971 Die Große Bartfledermaus (Myotis brandti) (Eversmann, 1845) in Jutland / Danemark (Vorlaufige Mitteilung) *Myotis* **9** 6–7

Ellerman J R & Morrison-Scott T C S 1951 *Checklist of Palaearctic and Indian mammals 1758 to 1946* London British Museum (Natural History), 810 pp

Eversmann E 1845 Vespertiliones, in promontoriis Uralensibus tractibusque confinibus observati *Bull Soc Imper Natur Moscou* **18** 489–516

Fairon J 1980 Myotis brandti en Belgique *Bull Inst Roy Sci Natur Belg* **52** 1–8

Fedorov A Ju 1978 Myotis brandtii (Eversmann, 1845) (Chiroptera, Vespertilionidae) in the Far East of the USSR *Zool Žurnal* **57** 1281–1284 (in Russian, English summ)

Feriancova-Masárova Z & Hanak V 1965 *Stavovce Slovenska IV Cicavce* [*Vertebrates of Slovakia IV Mammals*] Bratislava Vydavatel'stvo Slovenskej akademie vied, 334 pp (in Slovak)

Fernandez R & Ibanez C 1989 Patterns of distribution of bats in the Iberian Peninsula Pp 357–361 In Hanak V, Horaček I & Gaisler J (eds) *European Bat Research 1987* Praha Charles Univ Press, 718 pp

Findley J S 1972 Phenetic relationships among bats of the genus Myotis *Syst Zool* **21** 31–52

Gauckler A & Kraus M 1970 Kennzeichen und Verbreitung von Myotis brandti (Eversman, 1845) *Ztschr Saugetierk* **35** 113–124

Godawa Stormark J 1998 Phenetic analysis of Old World Myotis (Chiroptera Vespertilionidae) based on dental characters *Acta Theriol* **43** 1–11

Grimmberger E 1993 Beitrag zur Fledermausfauna (Chiroptera) Bulgariens und Rumaniens mit besonderer Berucksichtigung der Variabiltat der langflugelfledermaus (Miniopterus schreibersi Kuhl, 1819) *Nyctalus (N F)* 4(6) 623–634

Hackethal H 1982 Zur Merkmalsvariabilitat mitteleuropaischer Bartfledermause unter besonderer Berucksichtigung der Verbreitung und der okologischen Anspruche von Myotis brandti (Eversmann 1845) *Nyctalus (N F)* 1(4/5) 393–410

Haensel J 2000 Anmerkungen zu den deutschen Namen für die Arten der europaischen Fledermause *Nyctalus (N F)* 7(3) 287–290

Hanak V 1965 Zur Systematik der Bartfledermaus Myotis mystacinus Kuhl, 1819 und uber das Vorkommen von Myotis ikonnikovi Ognev, 1912 in Europa *Věst Čs Společ Zool* **29** 353–367

Hanak V 1967 Verzeichnis der Saugetiere der Tschechoslowakei *Saugetierk Mitt* **15** 193–221

Hanak V 1970 Notes on the distribution and systematics of Myotis mystacinus Kuhl, 1819 *Bijdr Dierk* **40** 40–44

Hanak V 1971 Myotis brandtii (Eversmann, 1845) (Vespertilionidae, Chiroptera) in der Tschechoslowakei *Věst Čs Společ Zool* **35** 175–185

Harrison D L 1963 Report on a collection of bats (Microchiroptera) from NW Iran *Ztschr Saugetierk* **28** 301–308

Hasbenli A 1997 Contributions to bat flies of Turkey (Diptera Nycteribiidae, Streblidae) *J Inst Sci Tech, Gazi Univ* **10** 533–544

Heinrich G 1936 Ueber die von mir im Jahre 1935 in Bulgarien gesammelten Saugetiere *Mitt Konigl Naturwiss Inst Sofia* **9** 33–48

Helversen O v 1989a New records of bats (Chiroptera) from Turkey *Zool Middle East* **3** 5–18

Helversen O v 1989b Bestimmungsslussel für die europaischen Fledermause nach ausseren Merkmalen *Myotis* **27** 41 60

Hill J E 1983 Bats (Mammalia Chiroptera) from Indo-Australia *Bull Br Mus Natur Histor (Zool)* **45** 103–208

Horaček I 1979 Comments on methods in craniomorphological studies in bats *Lynx, n s* **20** 111–112 (in Czech, English summ)

Horaček I & Hanak V 1984 Comments on the systematics and phylogeny of Myotis nattereri (Kuhl, 1818) *Myotis* **21–22** 20–29

Horáček I, Červeny J, Taušl A & Vítek D 1974 Notes on the mammal fauna of Bulgaria (Insectivora, Chiroptera, Rodentia) *Věst Čs Společ Zool* **38** 19–31

Horaček I, Hanak V & Gaisler J in press Bats of the Palearctic Region a taxonomic and biogeographic review *Proceedings of the VIIIth European Bat Research Symposium* Krakow

Hurka K 1972 Basilia mongolensis nudior subsp n nebst Bemerkungen zur Nycteribien- und Streblidenfauna Thrakiens (Diptera Pupipara) *Ann Naturhistor Mus Wien* **76** 709–713

Hurka K 1984 New taxa and new records of Palearctic Nycteribiidae and Streblidae (Diptera Pupipara) *Věst Čs Společ Zool* **48** 90–101

Ibanez C 1988 Notes on bats from Morocco Mammalia **52** *278–281*

Ibanez C, Guillen A, Fernadéz R, Perez J L & Guerrero S I 1992 Iberian distribution of some little known bat species *Mammalia* **56** 433–444

ICZN 1999 *International Code of Zoological Nomenclature* London International Trust for Zoological Nomenclature, 306 pp

Ilyin V Yu, Strelkov P P & Smirnov D G 1998 New records of bats from a central part of the Northern Caucasus *Plecotus et al* **1** 55–60 (in Russian, English summ)

Ivanova T 1998 First data on bats of Central Balkan Mts (Bulgaria) *Vespertilio* **3** 29–36

Kahmann H & Goerner P 1956 Les chiroptères de Corse *Mammalia* **20** 333–389

Kaščenko N F 1905 [Review of mammals from Western Siberia and Turkestan Part I Bats, Insectivores] *Izv Tomsk Univ* **27** 10–49 (in Russian)

Kock D 1984 Basilia mongolensis nudior Hurka 1972 in Österreich (Insecta Diptera Nycteribiidae) *Senckenbergiana Biol* **65** 43–46

Kock D 2000 Korrekte Schreibweisen wissenschaflicher Namen und Bezeichnung europaischer Fledermausarten *Nyctalus (N F)* 7(4) 451–452

Koopman K F 1993 Order Chiroptera Pp 137–241 In Wilson D E & Reeder D M (eds) *Mammal species of the world a taxonomic and geographic reference Second edition* Washington-London Smithsonian Inst Press, 1206 pp

Koopman K F 1994 *Chiroptera Systematics Handbook of Zoology, Volume VIII Mammalia, Part 60* Berlin-New York Walter de Gruyter, 217 pp

Kormilicina V V 1977 [Rare species of bats in the south of Krasnodar region] Pp 55–56 In *Materialy II Vsesojuznogo Soveščanija po Mlekopitajuščim* Moskva (in Russian)

Kostron K 1943 Myotis coluotus sp nov ein neuer Handflugler aus dem nordmahrischen Karste *Rozpr II Tř Čes Akad* **52**(17) 1–34, pl 1–5

Kruskop S V 1998 Difference in wing shape between species of whiskered bats (Selysius, Vespertilionidae) *Myotis* **36** 101–104

Kruskop S V & Borissenko A V 1996 A new subspecies of Myotis mystacinus (Vespertilionidae, Chiroptera) from East Asia *Acta Theriol* **41** 331–335

Kryštufek B & Červeny J 1997 New and noteworthy records of bats in Slovenia *Myotis* **35** 89–93

Kuhl H 1817 *Die deutschen Fledermause* Hanau privately published, 67 pp

Kuhl H 1819 Die deutschen Fledermause *Ann Wetter Ges Ges Naturk Hanau* **1**(2) 185–215

Kusjakin A P 1935 Neue Angaben uber Systematik und geographische Verbreitung der Fledermause (Chiroptera) der U d S S R *Bull Soc Natur Moscou S Biol* **44** 428–438 (in Russian, German summ)

Kuzjakin A P 1934 The bats from Tashkent and systematical remarks on some Chiroptera from Caucasus, Buchara and Turkmenia *Bull Soc Natur Moscou S Biol* **43** 316–330 (in Russian, English summ)

Kuzjakin A P 1950 *Letučie myši (Sistematika, obraz žizni i pol za dlja sel skogo hozjajstva)* [*Bats (Systematics, survey of biology and of importance for agricultural and forest eonomy)*] Moskva Sovetskaja nauka, 444 pp (in Russian)

Kuzjakin 1965 Otrjad rukokrylye Ordo Chiroptera [Order bats Ordo Chiroptera] Pp 79–116 In Bobrinskij N A Kuznecov B A & Kuzjakin A P 1965 *Opredelitel mlekopitajuščih SSSR* [*Key to identification of mammals of the USSR*] Moskva Prosveščenie, 382 pp (in Russian)

Kvartirnikov M A 1957 [Bats of Bulgaria Two new species for our fauna] *Priroda, Sofija* **6** 63–64 (in Bulgarian)

Martino V 1939 Materials for the ecology and zoogeography of the mammals of S Serbia *Zap Russ Nauč Inst , Belgrad* **14** 85–106 (in Russian, English summ)

Mendelssohn H & Yom-Tov Y 1999 *Fauna Palestina Mammalia of Israel* Jerusalem The Israel Academy of Sciences and Humanities, 440 pp + 37 pl

Menu H 1987 Morphotypes dentaires actuels et fossiles des chiroptères Vespertilioninés II Partie implications systematiues et phylogenetiques *Paleovertebrata* **17** 77–150

Menu H & Popelard J -B 1987 Utilisation des caractéres dentaires pour la determination des Vespertilionines de l'ouest Europeen *Le Rhinolophe* **4** 1–88

Miller G S 1912 *Catalogue of the Mammals of Western Europe (Europe exclusive Russia)* London Order of the Trustees of British Museum (Natural History), 1020 pp

Misonne X 1959 Analyse zoogeographique des mammifères de l'Iran *Mem Inst Roy Sci Natur Belg , II Ser* **59** 1–157

Mitchel-Jones A J , Amori G Bogdanowicz W , Kryštufek B , Reijnders P J H , Spitzenberger F , Stubbe M , Thissen J B M , Vohralik V & Zima J , 1999 *The Atlas of European Mammals* London Academic Press, 484 pp

Mošansky A & Gaisler J 1965 Ein Beitrag zur Erforschung der Chiropterenfauna der Hohen Tatra *Bonn Zool Beitr* **16** 249–267

Nemeth A 1993 *Untersuchungen zur der Phylogenie der europaischer Bartfledermause anhand mitochondrialer DNA-Seqeunzen* Unpubl Diplomarbeit, Friedrich-Alexander-Universitat Erlangen-Nurnberg

Nemeth A & Helversen O v 1993 The phylogeny of the Myotis mystacinus-group a molecular approach P 38 In Palmeirim J M , Rodriguez L & Rabaça J (eds) *VI European Bat Research Symposium Evora, Portugal, 22–27 August 1993 Programme, Abstracts, List of Participants* Évora Univ of Évora, 65 pp

Ogneff S I & Heptner W G 1928 Einige Mitteilungen uber die Saugetiere des mittleren Kopet-Dag und der anliegenden Ebene (Russisch-Turkestan) *Zool Anz* **75** 258–266

Ognev S J 1911 Sur une collection des mammifères, provenant de la province de l'Ussuri *Ann Mus Zool Acad Sci St -Petersb* **16** 475–511 (in Russian, French title)

Ognev S I 1927 A synopsis of Russian bats *J Mamm* **8** 140–157

Ognev S I 1928 *Zveri vostočnoj Evropy i severnoj Azii Tom pervyj Nasekomojadnye i letučie myši* [*The beasts of Eastern Europe and Northern Asia Insectivores and Bats*] Moskva-Leningrad Gosudarstvennoe Izdatel'stvo, 631 pp (in Russian)

Pandurska R S & Beshkov V A 1998 Species diversity of bats in underground roosts of the Western Stara Planina Mts (Bulgaria) *Vespertilio* **3** 81–91

Panouse J B 1953 Observations sur les chauves-souris du Maroc et addition d'une nouvelle espèce Myotis mystacinus (Kuhl 1819) a la faune marocaine *Bull Soc Sci Natur Maroc* **33** 89–107

Pavlinov I Ja & Rossolimo O L 1987 [Systematics of mammals of the USSR] *Sbor Trudov Zool Muz MGU* **25** 1–284 (in Russian)

Pavlinov I Ja & Rossolimo O L 1998 [Systematics of mammals of the USSR Additions] *Sbor Trudov Zool Muz MGU* **38** 1-192 (in Russian)

Pavlinov I Ja, Borisenko A V, Kruskop S V & Jahontov E L 1995 [Mammals of Eurasia II Non-Rodentia Systematic-geographical review] *Sbor Trudov Zool Muz MGU* **33** 1–336 (in Russian)

Peters W 1869 Bemerkungen uber neue oder weniger bekannte Flederthiere, besonders des Pariser Museums *Monatsber Konigl Akad Wissensch Berlin* **1869** 391–406

Petrov B M 1967 [On distribution of Myotis mystacinus Kuhl 1819 (Chiroptera, Mammalia) in Yugoslavia] *Arch Biol Sci, Belgrade* **19**(1–2) 9*P*–10*P* (in Serbo-Croatian)

Řehák Z & Beneš B 1996 *Contribution to the roost ecology of Myotis brandtii (Mammalia Chiroptera) in the* Czech Republic and Slovakia *Acta Soc Zool Bohem* **60** 51–56

Roer H 1975 Zur Verbreitung und Okologie der Großen Bartfledermaus, Myotis brandti (Eversmann, 1845), im mitteleuropaischen Raum *Saugetierk Mitt* **23** 138–143

Rossolimo O L & Pavlinov I Ja 1979 [Catalogue of type specimens of mammals in collection of Zoological Museum Moscow State University] *Sbor Trudov Zool Muz MGU* **18** 5–43 (in Russian)

Ruprecht A L 1974 The occurrence of Myotis brandtii (Eversmann, 1845) in Poland *Acta Theriol* **19** 81–90

Rybář P 1976 A craniometric comparison of holocene populations of Myotis mystacinus (Kuhl, 1817) and M *brandtii (Eversmann, 1845) (Chiroptera Mammalia)* *Bijdr Dierk* **46** 71–79

Schulz J 1995 *Die Okozonen der Erde Die okologische Gliederung der Geosphare 2, uberarbeitete Auflage* Stuttgart Ulmer Verlag, 536 pp

Steiner H M & Gaisler J 1994 On a collection of bats (Chiroptera) from NE Turkey and N Iran *Acta Sci Natur Brno* **28**(1) 1–37

Strelkov P P *1963 II Otrjad Chiroptera* - rukokrylye [*II Order Chiroptera* – bats] Pp 122–218 *In* Gromov I M, Gureev A A, Novikov G A, Sokolov I I, Strelkov P P & Čapskij K K 1963 *Mlekopitajuščie fauny SSSR Čast I* [*Mammals of the fauna of the USSR Part I*] Moskva-Leningrad Izdatel'stvo AN SSSR, 640 pp (in Russian)

Strelkov P P 1983a Myotis mystacinus and Myotis brandti in the USSR and interrelations of these species Part 2 *Zool Žurnal* **62** 259–270 (in Russian, English summ)

Strelkov P P 1983b [Record localities of Myotis brandti Eversmann, 1845 and Myotis mystacinus Kuhl, 1819 (Chiroptera, Vespertilionidae) based on collections from museums of the USSR] *Trudy Zool Inst AN SSSR* **119** 38–42 (in Russian)

Strelkov P P 1989 New data on the structure of baculum in Palaearctic bats 1 The genera Myotis, Plecotus, and Barbastella Pp 87–94 In Hanák V Horáček I & Gaisler J (eds) *European Bat Research 1987* Praha Charles Univ Press, 718 pp

Strelkov P P & Buntova E G 1982 Myotis mystacinus and M brandti (Chiroptera, Vespertilionidae) and interrelations of these species Part I *Zool Žurnal* **61** 1227–1241 (in Russian, English summ)

Strelkov P P & Šajmardanov R T 1983 [New data on the distribution of bats (Chiroptera) in Kazakhstan] *Trudy Zool Inst AN SSSR* **119** 3–37 (in Russian)

Stubbe M & Chotolchu N 1968 *Zur Saugetierfauna der Mongolei Ergebnisse der Mongolisch-Deutschen* Biologischen Expeditionen seit 1962, Nr 30 *Mitt Zool Mus Berlin* **44** 5–121

Švecov Ju G, Smirnov M N & Monahov G I 1984 *Mlekopitajuščie bassejna ozera Bajkal* [*Mammals of the Baikal Lake basin*] Novosibirsk Nauka, 258 pp (in Russian)

Tate G H H 1941 Results of the Archbold Expeditions No 39 A review of the genus Myotis (Chiroptera) of Eurasia, with special reference to species occurring in the East Indies *Bull Am Mus Natur Histor* **78** 537–565

Thomas O 1926 A new Myotis from Ladak *Ann Mag Natur Histor* **17** 609–610

Tiunov M P 1984 II Otrjad Chiroptera Blumenbach, 1779 – Rukokrylye [II Order Chiroptera Blumenbach 1779 – Bats] Pp 73–101 *In* Krivoševev V G (ed) *Nazemnye mlekopitajuščie Dal nego Vostoka SSSR Opredelitel* [*Land Mammals of the Far East of the USSR The Key*] Moskva Nauka, 358 pp (in Russian)

Tiunov M P 1997 *Bats of the Far East of Russia* Vladivostok Dalnauka, 134 pp (in Russian, English summ)

Topál G 1958 Morphological studies on the os penis of bats in the Carpathian Basin *Ann Histor-Natur Mus Natn Hung* **50** 331-342

Tsytsulina K A 1999 Geographic variation of Myotis mystacinus group in the Caucasus Region P 65 In Cruz M & Kazakiewicz K (eds) *VIIIth European Bat Research Symposium Abstracts* Krakow CIC and IASE PAS 88 pp

Tsytsulina K in press *Taxonomic status of Myotis ikonnikovi (Chiroptera, Vespertilionidae) and its relationships with similar species* *Acta Chiropterol* **3**

Tupinier Y & Aellen V 1978 Presence de Myotis brandti (Eversmann, 1845) (Chiroptera) en France et en Suisse *Rev Suisse Zool* **85** 449–456

Valenciuc N 1971 {Myotis ikonnikovi Ognev, 1911 et Nyctalus leisleri Kuhl 1818 (Chiroptera), espèces nouvelles por la Moldavie} *Stud Comun , Bacau* **4** 333–336 (in Romanian, French summ)

Vlček M 1970 Die Morphologie des Bakulum bei Fledermausen der Gattung Myotis *Prace a Studie - Přir , Pardubice* **2** 97–127 (in Czech, German summ)

Volleth M 1987 Differences in the location of nucleolus organizer regions in European vespertilionid bats *Cytogenet Cell Genet* **44** 186–197

Volleth M 1989 *Karyotypevolution und Phylogenie der Vespertilionidae (Mammalia Chiroptera)* Unpubl Doktor-Dissertation, Friedrich-Alexander-Universitat Erlangen-Nurnberg, 262 pp

Walter W 1972 Erster Lebenfund der Fledermausart Myotis brandti (Eversmann, 1845) in Osterreich *Die Hohle* **23** 59–60

Won C & Smith K G 1999 History and current status of mammals of the Korean Peninsula *Mamm Rev* **29** 3–33

Woodman N 1993 The correct gender of mammalian generic names ending in -otis *J Mamm* **74** 544–546

Yongzu Z , Sangke J , Guoqiang Q , Shiahau L , Zhongyao Y , Fenggui W & Manli Z 1997 *Distribution of Mammalian Species in China* Beijing China Forestry Publishing House, 280 pp

Yoon M H & Son S W 1989 Studies on taxonomy and phylogeny of bats inhabiting Korea I Taxonomical review of one Rhinolophid and six Vespertilionid bats *Korean J Zool* **32** 375–392

Yoshiyuki M 1989 *A Systematic Study of the Japanese Chiroptera* Tokyo National Science Museum, 242 pp

Yoshiyuki M 1993 Taxonomic analaysis of two species of Myotis (Chiroptera, Vespertilionidae) from eastern areas of Hokkaido, Japan *Mem Natn Sci Mus , Tokyo* **26** 135–141

Zava B & Violani C 1992 Nuovi dati sulla chirotterofauna italiana *Boll Mus Reg Sci Natur Torino* **10** 261–264

APPENDIX I

A revised list of the *Myotis mystacinus* group in the Palearctic: a preliminary version

This list includes species and subspecies of the *Myotis mystacinus* group, except for those from Japan The classification of the bats from the western Palearctic follows the results as discussed above, while the classification of bats from the eastern part of the Palearctic is a preliminary only (on the base of examination of the type material, see Discussion) The latter taxa are marked with an asterisk (*)

brandtii subgroup	
***Myotis brandtii* (Eversmann, 1845)**	Palearctic forests
Myotis brandtii brandtii (Eversmann, 1845)	W-Europe to W-Siberia (?) N part of the Far East
syn *Vespertilio Brandtii* Eversmann, 1845	
Vespertilio mystacinus sibiricus Kaščenko 1905	
Myotis coluotus Kostroň, 1943	
**Myotis brandtii gracilis* Ognev, 1927	SE part of range (from central Siberia to Far East)
syn **Myotis mystacinus gracilis* Ognev, 1927	
mystacinus subgroup	
***Myotis mystacinus* (Kuhl, 1817)**	European mixed forests, Mediterranean, Caucasus regs
Myotis mystacinus mystacinus (Kuhl, 1817)	European mixed forests (from Ireland to Ural Mts)
syn *Vespertilio mystacinus* Kuhl 1817	
Vespertilio mystacinus var *nigricans* Fatio, 1869	
Vespertilio lugubris Fatio, 1869	
Myotis mystacinus occidentalis Benda ssp. n.	western Mediterranean (Iberia and Morocco)
Myotis mystacinus caucasicus Tsytsulina ssp. n.	forests of the Caucasus region
***Myotis ikonnikovi* Ognev, 1911**	east-Palearctic mixed forests
nipalensis subgroup	
***Myotis aurascens* Kusjakin, 1935 stat. n.**	Palearctic steppes
Myotis aurascens aurascens Kusjakin, 1935 stat n	Central Mediterranean to E-European steppes
syn *Myotis mystacinus aurascens* Kusjakin, 1935	
Myotis mystacinus bulgaricus Heinrich, 1936	
Myotis mystacinus popovi Strelkov, 1983	

**Myotis aurascens mongolicus* Kruskop et Borissenko, 1996	mountain steppes of Central Asia
syn *Myotis mystacinus mongolicus* Kruskop et Borissenko, 1996	
***Myotis hajastanicus* Argyropulo, 1939 stat. n.**	Basin of the Sevan Lake, Armenia
syn *Myotis mystacinus hajastanicus* Argyropulo, 1939	
***Myotis nipalensis* (Dobson, 1871) stat. n.**	arid zone of Middle and Central Asia
Myotis nipalensis nipalensis (Dobson, 1871) stat. n.	N-Indian Mts (from Kashmir to Meghalaya)
syn *Vespertilio nipalensis* Dobson, 1871	
Myotis meinertzhageni Thomas, 1926	
Myotis nipalensis przewalskii Bobrinskoj, 1926 stat. n.	mountains and plateaus of Central Asia
syn *Myotis mystacinus przewalskii* Bobrinskoj, 1926	
**Myotis mystacinus kukunorensis* Bobrinskoj, 1929	
**Myotis mystacinus pamirensis* Kusjakin, 1935	
Myotis nipalensis transcaspicus Ogneff et Heptner, 1928 stat. n	deserts of Middle Asia
syn *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928	
Myotis mystacinus transcaspicus Ognev, 1928	
**Myotis mystacinus sogdianus* Kuzjakin, 1934	

Taxa incertae sedis (generally considered as unidentified synonymes of names *V mystacinus* or *V Brandtii*)
Vespertilio collaris Schinz, 1821
Vespertilio humeralis Baillon, 1834
Vespertilio schinzii Brehm, 1837
Vespertilio schrankii Wagner, 1843
Brachyotus mystacinus var *nigricans* Koch, 1865
Brachyotus mystacinus var *rufofuscus* Koch, 1865
Brachyotus mystacinus var *aureus* Koch, 1865
Vespertilio mystacinus var *nigrofuscus* Fitzinger, 1871

APPENDIX II – EXAMINED MATERIAL

In the presented list of examined material, collection and sample abbreviations were used, for explanation see pp 335–336 Other abbreviations f – female, m – male, s i – sex indefined All listed data correspond to specimen labels of the respective collection

Myotis brandtii (Eversmann, 1845)

AUSTRIA [AU] **Austria** Lower Austria Auzing (Gem Wurmla) [NMW 1f], Großschonau [NMW 1f], Kirchberg/Wechsel, Hermanshohle [NMW 1m, 2f], Schwarzenbach/Pielach, Trockenes Loch [NMW 1m] Vienna Wien 13, Hietzing [NMW 1m], Wien 23, Liesing [NMW 1f] Upper Austria Kreideluche, Hinterstoder [NMW 1m], Sankt Ulrich (n Steyr) [NMW 1f], Trannstein, Gmunden [NMW 1m], Wels [NMW 1f], Vorarlberg Bezau, Schonenbach, Schneckenloch [NMW 3m]
BOHEMIA [BO] **Czech Rep** Bila Desna (Liberec Dist) [NMP 4m, 2f], Bychory (Kolin Dist) [NMP 2f], Karlštejn (Beroun Dist) [NMP 1f], Mikulov (Teplice Dist) [NMP 2m], Poteply (Beroun Dist) [NMP 1f], Praha, Stare Město [NMP 1f], Ptice (Kladno Dist) [NMP 1 s i], Vůznice u Nove Huti (Přibram Dist) [NMP 1f], Vyžlovka u Jevan (Kolin Dist) [NMP 1f], Zdemyslice u Blovic (Plzeň-jih Dist) [NMP 1f] **Germany** (Saxonia) Rehfeld [NMP 1m]
MORAVIA [MA] **Czech Rep.** Běla pod Pradědem (Jeseník Dist) [SMO 4m], Lipová, jeskyně Na Pomezi cave (Jesenik Dist) [SMO 1m] Hlavnice (Opava Dist) [SMO 2m], Kobeřice (Opava Dist) [SMO 7f], Zalužna (Opava Dist) [SMO 1m], Kralicky Sněžnik Pachtova jeskyně cave (Usti nad Orlici Dist) [NMP 1m]
SLOVAKIA [SK] ***Slovakia*** *Dobšina, Dobšinska ľadova jaskyňa cave (Rožňava Dist) [NMP 17m, 3f, 1 s i], Horny* Turček (Turčianske Teplice Dist) (= Turček, Martin Dist , sensu Řehák & Beneš 1996) [SMO 1m, 8f]
NORTHERN BALKANS [BL] **Bulgaria** Gela (Smoljan Dist), 1350 m [NMP 5m], Hristo Danovo (Plovdiv Dist), Mazata peštera cave [ZMS 1m], Ladenica (Smoljan Dist) [NMP 1m], Murgaš hut (Stara Planina) (Sofija Dist) [ZMS 1m, 1f] **Montenegro** Ćakor, alt 1800 m [ZIN 1m]
CAUCASUS REGION [CA] **Georgia** Bakuriani [ZIN 1m] **Russia** Karačaevo-Čerkesskaja Rep Teberda [ZIN 1m] Krasnodarskij Kraj Reg Pšiš river [ZIN 1m, 1f], Psebaj [ZIN 1m] Caucasus Mts (loc undef) [ZIN 2f]
NORTHERN BALTIC REGION [BT] **Estonia** Paaskula (Tartu Dist) [ZIN 1m] **Finland** Padasjoki (Hameen Laani Dist) [NMW 1f] **Russia** Leningrad Reg Zamovšy-Ol'tyno [ZIN 1 s i], Sablino, Sablinskie peščery caves [ZIN 1m, 6f], Staraja Ladoga, Ladožskie caves [NMP 2m, 2f, ZIN 4f, 1 s i], Leningrad Reg (loc undef) [ZIN 3 s i]

Central Russia and Ural Region [RU] **Russia** Baškortostan Reg Kuešta (Iglinskij Dist) [ZIN 1m] Perm Reg Kamertskij Dist [ZIN 1f] Moskva Reg Kamkino (Podol'sk Dist) [ZIN 1f], Možajsk Dist [NMW 1m] Orenburg Reg Spask (= Spasskoe), 100 km VSV ot Orenburga [ZIN 3 s i = lectotype paralectotype and specimens of *Vespertilio Brandtii* Eversmann, 1845] Penza Reg Kurilovka, Sura river [ZIN 1f], Skanovskaja cave (*Narovčat Dist) [ZIN 1m], Virga (Nižnij Lomov Dist) [ZIN 1m]* Samara Reg Žiguljevskij Zapovednik Reserve [ZIN 1f] Tver' Reg Starica, 3 km N [NMW 1f] Voronež Reg "Bieberschutzgebiet" [NMW 1 s i], Voronežskij Zapovednik Reserve [ZIN 1m, 1f, 3 s i]

Other material examined **Lithuania** **Kaunas, IV fortas** [ZIN 1 s i] **Croatia** Uviraljka, Papuk Mts [ZIN 1m]

Myotis ikonnikovi Ognev, 1911

Material examined **China** *Manchuria, Mudandzen' river, Sungari [ZIN 1 s i]* **Kazakhstan** *Altaj*, Tigeretskij Range, Talovka river, mouth of Uba river [ZIN 1f] **Mongolia** SE-Mongolia, south of Eastern Hingan Mts , Dolon-Nor Lake [ZIN 1 s i] **Russia** Baikal Lake [ZIN 1 s i], Baikal Lake, Marituj, "springs of the Angara river" [ZIN 1m], Burjatia Rep Baikal Lake, Svjatoj Nos isthmus [NMP 7m, 3f, 5 s i] Irkutsk Reg Sahir (Zerenhovo Dist) [ZIN 1f] Orlenga river [ZMMU 2 s i] Krasnojarsk Reg Stolby Zapovednik Reserve, kordon Imtul [ZIN 1 s i], Prisk, Mišiha river [ZIN 1m] Primorskij Kraj Reg Evseevka village, 27 versts to SE Hanka Lake (Imanskij Uezd Dist) [ZMMU 1f = lectotype spec of *Myotis ikonnikovi* Ognev, 1911, ZIN 1f = paralectotype spec of *M ikonnikovi*], "Primorie" (loc undef) [ZIN 1 s i], Kangauz ("Ussurijskij Kraj") [ZIN 1f]

Myotis mystacinus (Kuhl, 1817)

Morocco [MO] **Morocco** Puente Fomento, 5 km NW Chechaouen [EBD 4f]

Spain [SP] **Spain** La Rioja El Rasillo, Cueva Carauco [EBD 1m] Salamanca Linares de Riofrio, [SMF 4m, 10f] Valencia Silla [SMF 1m]

England [EN] **United Kingdom** Dover [BMNH 1f], Manchester [BMNH 1m], Stratford-upon-Avon [BMNH 1 s i], England (loc undef) [BMNH 1 s i]

Central Alps [AL] **Austria** West Tirol Kappl [NMW 1f], Roppen [NMW 1f], Stollen in Jenbach [NMW 1m], Trins, Villa Marilaun [NMW 1m, 1f] Vorarlberg Bezau, Schonenbach, Schneckenloch [NMW 9m, 2f], Kennelbach [NMW 1f] **Germany** Baden-Wurtenberg Radolfzell, Bodensee [RMS 1m] Bavaria Allgau, Osterachtal, 1100 m [RMS 1m] **Switzerland** Sempach, Vogelraste [NMW 1 s i]

Austria [AU] **Austria** Burgenland Hammer b Lockenhaus [NMW 2f], Mattersburg [NMW 1f], Neudorfl [NMW 1m], Rust/Neusiedler See [NMW 1 s i], Sankt Michael i/B [NMW 1 s i] Lower Austria Asperhofen [NMW 1m], Horn [NMW 1f], Kirchberg am Wechsel [NMW 1 s i], Lunz am See [NMW 2m], Oed Oehling [NMW 1f], Pressbaum [NMW 1m] Upper Austria Kreideluche, Hinterstoder [NMW 1f], Sankt Ulrich bei Steyr [NMW 1m, 1f], Steyer [NMW 4m, 1f], Ternberg [NMW 2m] Styria Baierdorf bei Auger [NMW 1f], Ratten, Pretulalpe [NMW 1m], Gusswerk, Warwasschacht [NMW 1f], Hall [NMW 2m, 1 s i], Maria Buch-Fleistritz [NMW 1f], Naas [NMW 1m], Steinhaus am Semmering [NMW 1m], Tauplitz, Hohle am Seenplateau [NMW 1f], *Zeltweg [NMW 1m], Zirbitzhogel (Gem Granitzen) [NMW 1f]*

Bohemia [BO] **Czech Rep** Bila Desna (Liberec Dist) [NMP 2m], Chynov, Chynovska jeskyně cave (Tabor Dist) [NMP 2m], Dunajovice (Jindřichův Hradec Dist) [NMP 2f], Jindřichův Hradec (Jindřichův Hradec Dist) [NMP 2f], Karlštejn (Beroun Dist) [NMP 3m, 1f], Kersko (Kolin Dist) [NMP 1f], Lnaře (Strakonice Dist) [NMP 1m] Lomnice nad Lužnici (Jindřichův Hradec Dist) [NMP 5f, 1 s i], Mikulov u Teplic (Teplice Dist) [NMP 3m, 1f], Novosedly nad Nežarkou (Jindřichův Hradec Dist) [NMP 4f], Ustaleč (Klatovy Dist) [SMO 1m, 1f], Žirovnice (Pelhřimov Dist) [NMP 1 s i], Pec pod Sněžkou, Růžovy Důl, 850 m (Trutnov Dist) [NMP 1m] Poteply (Kladno Dist) [NMP 1f], *Dolni Počernice (Praha 10 Dist)* [NMP 1f], Třeboň, Novořecka bašta (Jindřichův Hradec Dist) [NMP 1f] **Germany** Upper Bavaria Nixloch, E Hallthurm [NMW 1f]

Moravia [MA] **Czech Rep** Běla pod Pradědem (Jesenik Dist) [SMO 1f], Kralicky Sněžnik, Pachtova jeskyně cave (Usti nad Orlici Dist) [NMP 1m], Lednice (Břeclav Dist) [NMP 3f], Lipova, jeskyně Na Pomezi cave (Jesenik Dist) [SMO 1m], Budišov nad Budišovkou (Opava Dist) [SMO 1m], Chvalikovice (Opava Dist) [SMO 1f], Smolkov (Opava Dist) [SMO 1m], Hlavnice (Opava Dist) [SMO 4f], Kobeřice (Opava Dist) [SMO 2f], Kružberska přehrada dam (Opava Dist) [sno 1f], Sadek (Opava Dist) [SMO 1m], Stěbořice (Opava Dist) [SMO 1f], Svitavy (Svitavy Dist) [NMP 1m], Velke Heraltice (Opava Dist) [SMO 2f]

Slovakia [SK] **Slovakia** jaskyňa Aksamitka cave (Stara Ľubovňa Dist) [NMP 1f], Demanovska dolina, Dračia jaskyňa cave [NMP 2m], Demanovska Dolina, Okno cave (Liptovsky Mikulaš Dist) [NMP 1f], Dobšina, Dobšinska ľadova jaskyňa (Rožňava Dist) [NMP 4m, 6f], Kraľovany, Bystrička valley (Dolny Kubin Dist) [NMP 1m], Muraň (dist Revuca) [NMP 1m]

South-Eastern Alps [EA] **Austria** Carinthia Althofen [NMW 1m], Dollach, Moelltal [NMW 1m], Lavamund [NMW 1m], Malta [NMW 1f], Sankt Georgen am Langsee [NMW 1 s i], Steindorf am Ossiacher See [NMW

1f], Waldorf G Maria Saal [NMW 1f], Willach, Eggerloch, Warmbad [NMW 1m], Winkel Heiligen blut [NMW 1m, 1f] East Tyrol Dollach, G Hopfgarten, Defreggental [NMW 1f], Schwarzach-Schlucht (Gem Matrei) [NMW 1m], Oberlienz [NMW 1f], Lienz [NMW 2m, 2f] **Slovenia** Bohinj Lake [PMS 1 s i], Ljubljana [PMS 1 s i], Koper, Škocjanski zatok [PMS 1 s i], Vrhnika (n Ljubljana) [PMS 1 s i] **Croatia** Sveti Rok [NMW 1m]

Northern Balkans [BL] **Bulgaria** Durankulak (Varna Dist) [SMO 1f], Čepelare (Smoljan Dist) [NMP 1m, 1f], Gela (Smoljan Dist) [NMP 6m, 1f], Gorna Breznica (Blagoevgrad Dist) [NMP 3m, 4f], Izgrev (Burgas Dist) [NMP 3m], Ladenica cave (n Gela) (Smoljan Dist) [NMP 2m], Pamporovo (Smoljan Dist) [NMP 1m] **Greece** Aliakmonas [OHC 1m], Ormylia (Halkidiki Dist) [NMP 1m], Potamos [OHC 1 s i] **Macedonia** Valandovo [PMS 1 s i], Strumica, 5 km SW [PMS 1f]

Ciscaucasia and Northern Caucasus Reg [CC] **Russia** Krasnodar Reg Adler [ZIN 1f], Aše [ZIN 1f], Gelendžik [ZMMU 1f], Hosta river, Kavkazskij Zapovednik Reserve [ZMSO 1 s i], Kavkazskij zapovednik Reserve (N-part), kordon Kiša [ZIN 1m], Psebaj, ca 10 km to E [ZIN 1m] Kabardino-Balkaria Rep Nal'čik [ZMMU 1m] Stavropol' Reg Stavropol' [ZIN 1f], Kislovodsk [ZMMU 1f] Severnaja Osetia Rep Vladikavkaz [ZIN 1f] N-Caucasus (undef) Estonian village n Ermolaevka [ZIN 1f]

Transcaucasia and the Great Armenia [TC] **Armenia** Erivan' (= Erevan) [ZIN 1f] **Azerbaijan** Agdam [NMP 1m], Hal'mil Dist [NMP 1m], Kutkašen [NMP 1 s i] **Georgia** Lagodehi [ZIN 1m] **Turkey** Aralik (Kars Dist) [ZIN 1m, 1f], Van (Van Dist) [NMP 1m]

Northern Baltic Reg [BT] **Finland** Loppi (Hammen Laani Dist) [NMW 1f] **Russia** Leningrad Reg Jamburg (= Kingisepp) [ZIN 1f], Kuznečnoe (Priozersk Dist) [ZIN 1f], Tajcy ("Petrogradskaja gubernija") [ZIN 1m] **Sweden** Ljusdal [RMS 2f]

Ural Region [UR] **Russia** Čeljabinsk Reg Staraja Serpievka (Kadavskij Dist) [ZIN 1m, 1 s i] Ekaterinburg Reg Middle Ural Mts (56°30'N, 59°35'E) [NMP 1m] Nižnyj Novgorod Reg Vasil'sursk, Volga river [ZIN 1 s i] Perm' Reg Div'ja cave (Nyrobskij Rajon Dist) [ZIN 1m] Samara Reg Samarskaja Luka [ZIN 6m, 1f] Volgograd Reg Berežnovka, left bank of the Volga river, mouth of the Eruslan river [ZIN 1f]

Other material examined **France** Corsica Solenzara [SMF 1m], Casamozza [SMF 1f]

Myotis aurascens Kusjakin, 1935

Dalmatia [DA] **Croatia** Brač I , Ložišće [ZZZ 1m], Dubrovnik, Soline [SMO 2f], Šolta I , Grohote [ZZZ 1m], Hvar I [ZZZ 1f], Korčula I , Čara [ZZZ 1f], Mljet I , Babino Polje, Vodice [ZZZ 2m, 4f], Scoglio Fernic, n Filipjakov (Zadar Dist) [NMW 3f], Šibenik, Ključ, Čikule canyon [ZZZ 1f], Tal des Jadro bei Salona/Solin oder Scoglio Barbato bei Jadro [NMW 2m, 7f]

Northern Balkans [BL] **Bulgaria** Beli Iskar dam (Rila Mts), 1900 m (Sofija Dist) [ZMS 1m], Čepelare, 1240 m (Smoljan Dist) [NMP 1m], Gara Tulovo n Kazanlak (Stara Zagora Dist) [NMP 1f], Gela, 1350 m (Smoljan Dist) [NMP 1m], Gorna Breznica (Blagoevgrad Dist) [NMP 7m, 13f], Hristo Danovo, Mazata cave (Plovdiv Dist) [ZMS m], Karlukovo (Loveč Dist) [NMP 1m], Kotel, Nirica cave (Sliven Dist) [NMP 1m], Momčilgrad (Kardžali Dist) [NMP 2f], Orehovo, Modarska peštera cave (Smoljan Dist) [ZMS 1m], Pasarel (Sofija Dist) [ZMS 1m, 1f], Philippopel (= Plovdiv, Plovdiv Dist) [BZM 2m = paratype specimens of *Myotis mystacinus bulgaricus* Heinrich, 1936, 1f = holotype spec of *M m bulgaricus*, MTD 1m = paratype spec of *M m bulgaricus*], Vodnite Dupki cave, Pleven hut (Gabrovo Dist) [ZMS 1m], Bulgaria (undef) [ZMS 1m, NMP 2 s i] **Greece** Arkoudorema (Rodopi Dist) [OHC 1m], Gramos (Kastoria Dist) [OHC 2m], Marathoussa (Halkidiki Dist) [OHC 1 s i], Metalion (Kilkis Dist) [OHC 1f], Metamorfosi (Halkidiki Dist) [NMP 1m], Neglei (Drama Dist) [OHC 1f], Nestorio, Aliakmonas river (Kastoria) [OHC 1f], Ormylia (Halkidiki Dist) [NMP 3f], Prionia n Litohoro, Olympos Mts (Pieria Dist) [NMP 1f] **Macedonia** Asamati, Kurbinovo [PMS 1m], Demir Kapija [PMS 1 s i], Nov Dojran [PMS 1 s i], Kočane (= Kočani) [ZIN 1 s i], Makedonski Brod, Grešnica [PMS 1f], Strumica, 5 km SW [PMS 1 s i], Valandovo [PMS 1f, 2 s i], Veleš, Crkvine, Markova kula [PMS 1 s i] Velmej 3 km E [PMS 1 s i] **Serbia (Kosovo)** Pec [ZIN 2 s i]

Ukraine [UA] **Moldavia** Bygok (Tiraspol' Dist) [ZIN 2f], vicinity of Kišinev [ZIN 1m, 1 s i], Malye Melešty, galleries [ZIN 1f = paratype spec of *Myotis mystacinus popovi* Strelkov, 1983], Moldavia (loc undef) [ZIN 2m, 1f = paratype specimens of *M m popovi*] **Ukraine** Doneck Reg Doneck Dist [ZMMU 1 s i = paratype specimen of *M m popovi*] Krym Reg (= Crimea) Karadag [ZIN 2m], Kerč' peninsula, vicinity of Kamenskoe [ZIN 1m = holotype spec of *M m popovi*], Tatakoj [ZIN 2 s i = paratype specimens of *M m popovi*], vicinity of Simferopol' [ZIN 1m, 2m = paratype specimens of *M m popovi*], Krym (= Crimea) (loc undef) [ZIN 1 s i] Herson Reg Kujuk-Tuk, Sivaš Bay [ZIN 1m, 2f] Odessa Reg Beljaevka Dist [ZIN 1m, 2f], Odessa Reg (loc undef) [ZIN 1m, 2f] Zaporož'e Reg Zaporož'e [ZMMU 1m, 3f], Bolgrad (Melitopol' Dist) [ZIN 1m] **Russia** "Oblast' Donskogo Vojska" (= Lower Don river Reg) [ZMMU 1f]

Lower Volga Region [LV] **Russia** Astrahan' Reg Astrahan' [ZIN m] Samara Reg Samarskaja Luka [ZIN 1f] Saratov Reg D'jakovka, Eruslan river (Krasnokutskij Dist) [ZIN 4f] Volgograd Reg Berežnovka, left bank of the Volga river, mouth of the Eruslan river [ZIN 2m, 7f], Nagornyj (Kamyšin Dist) [ZIN 1f]
Ciscaucasia and Northern Caucasus Reg [CC] **Russia** Čečenia Rep between Groznyj and Kizljar [ZIN 1f] Dagestan Rep Miusskij Dist [ZIN 1m], Dagestan (undef) [ZIN 1 s i] Krasnodar Reg Malyj Irtyš (Novorossijsk Dist) [ZIN 1f], Tuapse Dist [ZMMU 2f], st Tarasovka [ZMMU 1m = paratype specimen of *Myotis mystacinus popovi* Strelkov, 1983] Rostov-na-Donu Reg Tarasovskij Dist [ZMMU 1 s i] Severnaja Osetia Rep Kurkužin n Vladikavkaz [ZMMU 1m, 2f, incl holotype spec of *Myotis mystacinus aurascens* Kusjakin, 1935] Stavropol' Reg Kazarma (Ipatovo Dist) [ZIN 1f], between Levokumskoe and Aleksandrovskoe [ZIN 3f] Northern Caucasus Reg (undef) [ZMMU 2f]
Transcaucasia and the Great Armenia [TC] **Azerbaijan** "Elizavetpol'skaja Gubernija" [ZIN 1f] Geok-Tapa (= Port Il'jič) [ZIN 2f], Geokčaj river valley, 1460 m [NMP 1m] **Iran** Gutur Su (E-Azerbaijan Prov) [BMNH 3m] **Turkey** Sırbasan (Kars Dist) [NMP 1m] Van (Van Dist) [NMP 2m]
Other material examined **Italy** Mt Altissimo di Nago, Monte Baldo [SMF 1f] **Greece** Peloponnese, Kardamili (Mesinia Dist) [NMP 1f], Peloponnese, Sparta (Lakonia Dist) [NMP 1f], Crete, Stavros (Hania Dist) [NMP 1m] **Kazakhstan** Aktjubinskaja Oblast' Reg east bank of the Emba river, 125 km SEE Kul'sary [ZIN 3f], Karakol' Lake, Turgaj river valley [ZIN 1f]

M.* cf. *aurascens
material examined **Syria/Israel** Mt Hermon [TAU 1m] **Turkey** Beşkonkak (Antalya Dist) [OHC 1f] Sohun Dere (Erzurum Dist) [OHC 1m], Uçpınar n Bozkır (Konya Dist) [OHC 1f]

Myotis hajastanicus Argyropulo, 1939

Sevan Lake Basin [SB] **Armenia** Aparan [ZIN 2f], vicinity of Basargečar vill , n Karčahpjur, Sevan Lake Basin [ZIN 2f], vicinity of Čkalovka vill , Sevan Lake Basin [ZIN 3f], Šordža village, E bank of the Sevan Lake [NMP 2f = paratype specimens of *Myotis mystacinus hajastanicus* Argyropulo, 1939, ZIN 7f], Sevan Lake Basin (undef) [ZIN 1 s i]

Myotis nipalensis (Dobson, 1871)

Transcaucasia and the Great Armenia [TC] **Azerbaijan** "Elizavetpol'skaja Gubernija" [ZIN 1f], Geok-Tapa (= Port Il'jič) [ZIN 1f 1 s i], Mingečaur, Adžinar steppe [NMP 1f], Sal'jany, Kura river [ZIN 1 s i], Šeki Dist [NMP 1f] **Georgia** Lagodchi [ZIN 1m] **Iran** Bastam (W-Azerbaijan prov) [NMP 2m] **Turkey** Aralık (dist Kars) [ZIN 1m 1f, 2 s i], Sırbasan (Kars Dist) [NMP 1m]
Western Turkestan [TM] **Kazakhstan** Mangyšlak [ZIN 1 s i], Fort Aleksandrovskij (= Fort Ševčenko) [ZIN 1 s i] **Turkmenistan** Germad [ZMMU 1m = type spec of *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928], Hasan Kuli [NMP 1m, 1f, ZIN 10fa], Krasnovodsk (= Turkmenbaşı) [ZMMU 1f]
Eastern Turkestan [ET] **China** Southern Kashgaria, Mol'dža river valley [ZIN 4 s i = type series of *Myotis mystacinus przewalskii* Bobrinskoj, 1926]
Other material examined **India (Kashmir)** Dak Bungalow, Kokernag (as *M muricola* in Bates & Harrison 1997, but see Hill 1983) [BMNH 1f], junction of Nubra and Shyok rivers, Ladak [BMNH 1f = holotype spec of *Myotis meinertzhageni* Thomas, 1926] ? **India (Punjab)** Guggah, Nullah, Eashmere [BMNH 1 s i] **Kazakhstan** Aktjubinsk Reg east bank of the Emba river, 125 km SEE Kul'sary [ZIN 2f] **Tajikistan** Jašil'-Kul' Lake [ZMMU 1f = holotype spec of *Myotis mystacinus pamirensis* Kusjakin, 1935] **Uzbekistan** Taškent [ZMMU 1f = holotype spec of *Myotis mystacinus sogdianus* Kuzjakin, 1934]

APPENDIX III

Selected statistical parameters of the studied samples of bats (Tabs 1-11, pp 388-398) For the explanation see Abbreviations (p 336) Other abbreviations used *n* – number of specimens in the respective sample, min, max – minimum and maximum value of the respecive dimension, M – mean, SD – standard deviation

Tab 1 Measurements of *Myotis mystacinus* s l populations of the westernmost part of Palaearctic

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	Morocco [MO] (n = 4)					Spain [SP] (n = 16)					England [EN] (n = 4)				
LCr	*4*	13.53	14.10	**13.800**	0.278	*14*	13.23	14.07	**13.773**	0.212	*4*	13.00	13.62	**13.328**	0.313
LCb	*4*	12.78	13.37	**13.108**	0.289	*12*	12.68	13.52	**13.083**	0.245	*3*	12.25	12.92	**12.523**	0.352
LaZ	*4*	8.23	8.43	**8.330**	0.091	*4*	8.22	8.71	**8.373**	0.232	–	–	–	–	–
LaI	*4*	3.22	3.47	**3.370**	0.108	*16*	3.13	3.63	**3.415**	0.134	*4*	3.40	3.77	**3.518**	0.170
LaInf	*4*	3.16	3.35	**3.298**	0.092	*16*	2.98	3.48	**3.287**	0.128	*4*	3.10	3.42	**3.273**	0.149
LaN	*4*	6.60	6.80	**6.690**	0.092	*14*	6.34	6.83	**6.624**	0.133	*4*	6.27	6.71	**6.538**	0.190
ANc	*4*	4.75	4.82	**4.778**	0.030	*13*	4.44	4.90	**4.674**	0.133	*3*	4.50	4.60	**4.557**	0.051
ACr	*4*	5.83	6.05	**5.903**	0.104	*15*	5.62	6.00	**5.824**	0.134	*4*	5.53	5.85	**5.655**	0.137
CC	*4*	3.33	3.45	**3.370**	0.057	*15*	3.12	3.54	**3.399**	0.135	*4*	3.10	3.35	**3.270**	0.115
P^4P^4	*4*	4.40	4.63	**4.470**	0.109	*15*	4.05	4.72	**4.441**	0.157	*4*	4.10	4.45	**4.358**	0.172
M^3M^3	*4*	5.22	5.38	**5.305**	0.082	*15*	4.97	5.55	**5.255**	0.155	*3*	5.20	5.30	**5.260**	0.053
IM^3	*4*	6.02	6.37	**6.195**	0.176	*16*	6.08	6.48	**6.263**	0.119	*4*	5.83	6.28	**6.045**	0.238
CM^3	*4*	4.97	5.35	**5.173**	0.206	*16*	4.97	5.38	**5.184**	0.095	*4*	4.70	5.08	**4.920**	0.179
P^4M^3	*4*	3.74	3.95	**3.842**	0.096	*16*	3.68	3.90	**3.801**	0.074	–	–	–	–	–
M^1M^3	*4*	2.97	3.21	**3.105**	0.098	*16*	2.92	3.18	**3.067**	0.069	–	–	–	–	–
M^1M^2	*4*	2.29	2.38	**2.341**	0.430	*16*	2.25	2.48	**2.391**	0.059	–	–	–	–	–
CP^4	*4*	5.40	2.60	**2.504**	0.970	*16*	2.37	2.66	**2.511**	0.088	–	–	–	–	–
P^2P^3	*4*	0.75	0.77	**0.762**	0.005	*16*	0.62	0.86	**0.759**	0.065	–	–	–	–	–
LP^3	*4*	0.35	0.37	**0.356**	0.009	*16*	0.28	0.43	**0.352**	0.048	–	–	–	–	–
LMd	*4*	9.52	10.08	**9.805**	0.312	*14*	9.38	10.12	**9.838**	0.209	*4*	9.10	9.72	**9.363**	0.292
ACo	*4*	2.65	2.82	**2.728**	0.070	*13*	2.43	2.92	**2.728**	0.110	*4*	2.70	2.90	**2.793**	0.098
IM_3	*4*	6.37	6.77	**6.548**	0.186	*14*	6.47	6.80	**6.601**	0.100	*4*	5.95	6.60	**6.345**	0.286
CM_3	*4*	5.27	5.70	**5.480**	0.186	*15*	5.38	5.68	**5.555**	0.090	*4*	5.20	5.52	**5.363**	0.161
P_4M_3	*3*	3.97	4.21	**4.070**	0.124	*15*	3.97	4.24	**4.095**	0.080	–	–	–	–	–
M_1M_3	*3*	3.29	3.50	**3.368**	0.115	*15*	3.32	3.58	**3.425**	0.078	–	–	–	–	–
CP_4	*4*	2.12	2.40	**2.283**	0.127	*15*	2.14	2.35	**2.245**	0.068	–	–	–	–	–
P_2P_3	*4*	0.89	0.96	**0.927**	0.033	*15*	0.84	1.03	**0.903**	0.053	–	–	–	–	–
LP_3	*4*	0.39	0.45	**0.411**	0.028	*15*	0.35	0.43	**0.376**	0.026	–	–	–	–	–
LaP^4	*4*	1.23	1.33	**1.270**	0.046	*16*	1.11	1.34	**1.229**	0.055	–	–	–	–	–
LaM^1	*4*	1.35	1.44	**1.398**	0.036	*16*	1.33	1.49	**1.420**	0.040	–	–	–	–	–
LaM^2	*4*	1.50	1.62	**1.565**	0.052	*16*	1.54	1.68	**1.605**	0.044	–	–	–	–	–
LaM^3	*4*	1.46	1.55	**1.479**	0.048	*16*	1.37	1.57	**1.470**	0.050	–	–	–	–	–
ACin	*4*	0.02	0.08	**0.042**	0.028	*16*	0.04	0.15	**0.094**	0.030	–	–	–	–	–
LCn	–	–	–	–	–	*14*	0.85	1.01	**0.919**	0.044	–	–	–	–	–
LaCn	–	–	–	–	–	*14*	0.69	0.81	**0.737**	0.032	–	–	–	–	–
RCn	–	–	–	–	–	*14*	1.137	1.364	**1.249**	0.057	–	–	–	–	–
LAt	*3*	34.7	35.5	**35.20**	0.436	*16*	32.8	36.6	**34.73**	0.940	–	–	–	–	–
LPol	*4*	4.3	4.8	**4.55**	0.208	*16*	4.3	5.1	**4.73**	0.241	–	–	–	–	–
LMcV	*4*	29.9	31.3	**30.50**	0.606	*16*	26.7	31.4	**29.48**	1.673	–	–	–	–	–
LMcIV	*4*	29.8	31.9	**30.75**	0.911	*16*	27.5	32.1	**30.09**	1.431	–	–	–	–	–
LMcIII	*4*	30.8	33.2	**31.93**	1.005	*16*	27.8	32.6	**30.90**	1.472	–	–	–	–	–
LMcII	*4*	29.9	31.0	**30.45**	0.580	*16*	24.8	30.8	**28.73**	1.801	–	–	–	–	–
LPVp	*4*	6.9	7.8	**7.25**	0.387	*16*	7.2	8.5	**7.71**	0.440	–	–	–	–	–
LPVm	*4*	4.9	5.6	**5.23**	0.299	*16*	4.4	6.4	**5.57**	0.601	–	–	–	–	–
LPIVp	*4*	7.2	8.0	**7.60**	0.365	*16*	7.2	9.4	**8.13**	0.542	–	–	–	–	–
LPIVm	*4*	7.1	7.5	**7.33**	0.206	*16*	5.6	8.2	**6.89**	0.755	–	–	–	–	–
LPIIIp	*4*	9.9	10.4	**10.18**	0.222	*16*	9.3	13.9	**10.86**	1.101	–	–	–	–	–
LPIIIm	*4*	9.5	10.0	**9.73**	0.222	*16*	6.4	12.2	**9.26**	1.437	–	–	–	–	–
LTib	*4*	14.9	16.3	**15.73**	0.655	*16*	12.8	16.6	**14.90**	1.367	–	–	–	–	–

Tab 2 Measurements of *Myotis mystacinus* s l Alpine populations

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	Central Alps [AL] (n = 20)					Northern Austria [AU] (n = 35)					SE-Alps [EA] (n = 22)				
LCr	*18*	12.87	13.75	**13.414**	0.220	*35*	12.82	13.87	**13.357**	0.286	*19*	12.78	13.73	**13.328**	0.261
LCb	*18*	12.25	13.10	**12.748**	0.241	*35*	12.30	13.25	**12.717**	0.255	*20*	12.02	13.07	**12.616**	0.284
LaZ	*14*	8.05	8.53	**8.220**	0.132	*25*	7.73	8.53	**8.173**	0.239	*17*	7.82	8.25	**8.016**	0.127
LaI	*20*	3.17	3.60	**3.369**	0.113	*35*	3.20	3.60	**3.407**	0.111	*21*	3.07	3.58	**3.399**	0.135
LaInf	*20*	2.95	3.52	**3.213**	0.147	*35*	2.92	3.42	**3.167**	0.137	*22*	2.88	3.45	**3.177**	0.138
LaN	*18*	6.45	6.83	**6.679**	0.111	*32*	6.23	6.97	**6.596**	0.159	*20*	6.27	6.75	**6.560**	0.115
ANc	*19*	4.48	4.98	**4.707**	0.147	*35*	4.42	4.95	**4.635**	0.124	*20*	4.45	4.83	**4.665**	0.111
ACr	*10*	5.60	6.33	**5.847**	0.233	*26*	5.52	6.00	**5.770**	0.142	*14*	5.62	6.02	**5.773**	0.108
CC	*19*	3.25	3.62	**3.398**	0.084	*34*	2.93	3.57	**3.317**	0.156	*21*	2.92	3.50	**3.295**	0.149
P^4P^4	*19*	4.25	4.70	**4.448**	0.117	*35*	4.03	4.70	**4.356**	0.180	*22*	3.92	4.63	**4.351**	0.192
M^3M^3	*19*	5.00	5.42	**5.219**	0.123	*34*	4.88	5.50	**5.179**	0.191	*22*	4.70	5.47	**5.081**	0.180
IM^3	*18*	5.77	6.28	**6.103**	0.168	*35*	5.88	6.42	**6.093**	0.155	*21*	5.65	6.35	**6.036**	0.169
CM^3	*20*	4.73	5.20	**5.009**	0.143	*35*	4.73	5.28	**5.014**	0.138	*21*	4.77	5.25	**5.036**	0.124
P^4M^3	*20*	3.53	3.82	**3.704**	0.086	*35*	3.55	3.90	**3.715**	0.094	*22*	3.58	4.00	**3.750**	0.113
M^1M^3	*20*	2.87	3.16	**3.033**	0.074	*35*	2.82	3.21	**3.016**	0.090	*22*	2.87	3.26	**3.037**	0.090
M^1M^2	*20*	2.23	2.43	**2.321**	0.054	*35*	2.20	2.48	**2.338**	0.073	*22*	2.21	2.43	**2.336**	0.065
CP^4	*20*	2.26	2.60	**2.308**	0.110	*35*	2.26	2.62	**2.403**	0.100	*21*	2.20	2.55	**2.415**	0.094
P^2P^3	*20*	0.61	0.80	**0.741**	0.049	*35*	0.63	0.81	**0.742**	0.045	*20*	0.63	0.83	**0.738**	0.051
LP^3	*20*	0.28	0.41	**0.341**	0.033	*34*	0.29	0.41	**0.346**	0.028	*19*	0.29	0.39	**0.346**	0.029
LMd	*20*	8.92	9.70	**9.472**	0.221	*35*	9.08	10.10	**9.465**	0.233	*21*	9.13	9.82	**9.476**	0.224
ACo	*19*	2.35	2.82	**2.642**	0.103	*33*	2.42	2.82	**2.645**	0.107	*21*	2.38	2.85	**2.580**	0.129
IM_3	*17*	6.15	6.63	**6.421**	0.167	*35*	6.12	6.87	**6.438**	0.169	*20*	6.25	6.63	**6.428**	0.097
CM_3	*19*	5.10	5.59	**5.366**	0.148	*35*	5.15	5.67	**5.403**	0.127	*21*	5.20	5.58	**5.375**	0.102
P_4M_3	*19*	3.76	4.13	**3.954**	0.112	*35*	3.68	4.21	**3.992**	0.109	*21*	3.84	4.26	**4.026**	0.105
M_1M_3	*19*	3.18	3.42	**3.328**	0.065	*35*	3.24	3.53	**3.346**	0.079	*21*	3.24	3.63	**3.386**	0.094
CP_4	*20*	2.04	2.34	**2.213**	0.085	*35*	2.07	2.38	**2.216**	0.090	*21*	1.97	2.31	**2.183**	0.094
P_2P_3	*19*	0.86	1.02	**0.901**	0.042	*35*	0.80	0.98	**0.893**	0.044	*19*	0.83	0.93	**0.882**	0.030
LP_3	*19*	0.34	0.46	**0.394**	0.034	*35*	0.28	0.46	**0.386**	0.035	*20*	0.31	0.42	**0.381**	0.027
LaP^4	*20*	1.13	1.31	**1.223**	0.043	*35*	1.07	1.36	**1.201**	0.064	*22*	1.15	1.31	**1.218**	0.042
LaM^1	*20*	1.23	1.42	**1.377**	0.045	*35*	1.29	1.49	**1.376**	0.043	*22*	1.30	1.53	**1.384**	0.056
LaM^2	*20*	1.45	1.63	**1.552**	0.055	*35*	1.46	1.63	1.540	0.043	*22*	1.48	1.64	1.555	0.042
LaM^3	*20*	1.32	1.53	1.428	0.054	*35*	1.34	1.54	**1.429**	0.056	*22*	1.33	1.58	**1.439**	0.059
ACin	*20*	0.04	0.15	**0.086**	0.033	*34*	0.04	0.17	**0.103**	0.033	*21*	0.06	0.18	**0.111**	0.035
LCn	–	–	–	–	–	–	–	–	–	–	*5*	0.79	0.90	**0.838**	0.044
LaCn	–	–	–	–	–	–	–	–	–	–	*5*	0.60	0.72	**0.676**	0.050
RCn	–	–	–	–	–	–	–	–	–	–	*5*	1.179	1.316	**1.241**	0.049
LAt	*19*	32.4	35.7	**33.66**	0.906	*8*	32.7	34.8	**33.81**	0.751	*12*	32.8	35.0	**34.10**	0.785
LPol	*19*	4.5	5.3	**4.75**	0.198	*8*	4.2	5.4	**4.74**	0.407	*12*	4.4	5.1	**4.72**	0.225
LMcV	*19*	28.2	30.8	**29.43**	0.684	*8*	28.5	31.1	**29.50**	0.883	*12*	28.3	31.1	**29.83**	0.746
LMcIV	*19*	28.1	30.5	**29.35**	0.699	*8*	27.9	30.8	**29.10**	1.036	*12*	27.9	31.0	**29.82**	0.838
LMcIII	*19*	28.3	31.7	**30.44**	0.797	*8*	29.3	31.7	**30.40**	0.862	*12*	29.3	32.4	**31.04**	0.811
LMcII	*19*	26.9	30.7	**28.76**	1.046	*8*	26.9	30.0	**28.48**	1.103	*12*	27.3	30.5	**29.04**	0.939
LPVp	*19*	6.9	7.9	**7.42**	0.306	*8*	6.5	8.0	**7.35**	0.487	*12*	6.7	8.0	**7.28**	0.404
LPVm	*19*	4.5	6.1	**5.46**	0.376	*8*	4.7	6.4	**5.50**	0.661	*12*	4.4	6.1	**5.48**	0.529
LPIVp	*19*	6.8	8.5	**7.70**	0.480	*8*	7.3	8.1	**7.64**	0.320	*12*	7.1	8.2	**7.70**	0.362
LPIVm	*19*	6.4	8.3	**7.41**	0.543	*8*	6.2	9.7	**7.46**	1.140	*12*	6.4	8.1	**7.28**	0.566
LPIIIp	*19*	9.1	11.0	**10.03**	0.543	*8*	9.6	10.5	**9.99**	0.419	*12*	9.4	10.7	**10.24**	0.425
LPIIIm	*19*	8.3	10.6	**9.20**	0.669	*8*	8.0	10.7	**9.45**	0.952	*12*	8.5	10.3	**9.55**	0.434
LTib	*18*	12.3	15.9	**14.24**	0.904	*7*	13.7	14.8	**14.39**	0.389	*12*	13.4	14.7	**14.18**	0.393

Tab. 3. Measurements of *Myotis mystacinus* s. l. Central-European populations

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	Bohemia [BO] (n = 33)					Moravia [MA] (n = 25)					Slovakia [SK] (n = 15)				
LCr	33	12.76	13.86	**13.455**	0.268	23	12.70	13.91	**13.484**	0.316	15	13.28	13.93	**13.565**	0.176
LCb	33	12.17	13.28	**12.762**	0.278	21	12.03	13.55	**12.837**	0.348	15	12.62	13.20	**12.901**	0.152
LaZ	26	7.72	8.62	**8.181**	0.247	9	8.00	8.52	**8.194**	0.144	8	8.12	8.44	**8.825**	0.122
LaI	33	3.20	3.65	**3.408**	0.113	25	3.12	3.52	**3.380**	0.116	15	3.22	3.53	**3.410**	0.087
LaInf	33	2.98	3.39	**3.186**	0.108	25	2.88	3.42	**3.192**	0.128	15	2.99	3.33	**3.212**	0.093
LaN	33	6.27	6.97	**6.643**	0.154	25	6.05	6.83	**6.644**	0.162	15	6.37	6.75	**6.637**	0.108
ANc	33	4.32	5.03	**4.667**	0.163	23	4.45	4.92	**4.690**	0.135	15	4.53	5.05	4.744	0.131
ACr	30	5.44	6.02	**5.737**	0.150	20	5.42	6.13	**5.784**	0.182	13	5.60	6.05	**5.820**	0.111
CC	33	3.08	3.55	**3.305**	0.115	23	2.93	3.65	**3.298**	0.171	15	3.17	3.46	**3.339**	0.075
P^4P^4	33	4.07	4.70	**4.399**	0.150	25	4.02	4.65	**4.397**	0.165	15	4.13	4.53	**4.405**	0.103
M^3M^3	33	4.88	5.43	**5.192**	0.136	24	4.76	5.47	**5.203**	0.192	15	5.05	5.48	**5.219**	0.115
IM^3	33	5.78	6.42	**6.082**	0.163	25	5.55	6.54	**6.107**	0.173	15	6.02	6.23	**6.153**	0.070
CM^3	33	4.70	5.35	**5.014**	0.150	24	4.80	5.37	**5.045**	0.122	15	4.87	5.17	**5.075**	0.088
P^4M^3	33	3.53	3.92	**3.727**	0.108	25	3.47	3.95	**3.689**	0.106	15	3.58	3.92	**3.777**	0.083
M^1M^3	33	2.84	3.18	**3.010**	0.088	24	2.84	3.13	**2.971**	0.089	15	2.87	3.16	**3.042**	0.086
M^1M^2	33	2.20	2.48	**2.340**	0.069	25	2.20	2.45	**2.315**	0.066	15	2.18	2.46	**2.372**	0.076
CP^4	33	2.23	2.57	**2.411**	0.084	25	2.23	2.57	**2.386**	0.091	15	2.28	2.57	**2.485**	0.078
P^2P^3	31	0.64	0.85	**0.747**	0.046	25	0.64	0.85	**0.733**	0.052	15	0.66	0.81	**0.752**	0.042
LP^3	31	0.26	0.42	**0.349**	0.033	25	0.26	0.42	**0.337**	0.038	15	0.30	0.38	**0.341**	0.022
LMd	33	9.15	10.02	**9.595**	0.228	25	8.93	10.02	**9.594**	0.281	15	9.53	10.02	**9.737**	0.149
ACo	32	2.38	2.82	**2.623**	0.101	24	2.28	2.88	**2.697**	0.126	15	2.52	2.78	**2.659**	0.082
IM_3	33	6.13	6.75	**6.434**	0.151	25	5.77	6.87	**6.426**	0.195	15	6.34	6.65	**6.512**	0.091
CM_3	33	5.22	5.65	**5.407**	0.123	25	5.03	5.80	**5.392**	0.162	15	5.27	5.62	**5.463**	0.099
P_4M_3	32	3.71	4.21	**4.023**	0.120	25	3.68	4.21	**3.973**	0.139	15	3.74	4.24	**4.102**	0.102
M_1M_3	32	3.21	3.53	**3.374**	0.097	25	3.05	3.47	**3.299**	0.117	15	3.13	3.58	**3.419**	0.112
CP_4	33	2.04	2.35	**2.159**	0.076	25	1.81	2.40	**2.101**	0.149	15	2.07	2.35	**2.216**	0.075
P_2P_3	33	0.80	0.97	**0.877**	0.040	25	0.68	0.94	**0.830**	0.073	15	0.80	0.94	**0.867**	0.042
LP_3	33	0.33	0.43	**0.378**	0.027	25	0.28	0.43	**0.346**	0.035	15	0.30	0.43	**0.371**	0.033
LaP^4	32	1.06	1.30	**1.204**	0.058	12	1.11	1.29	**1.198**	0.047	15	1.12	1.23	**1.250**	0.043
LaM^1	32	1.25	1.51	**1.391**	0.058	12	1.31	1.16	**1.375**	0.045	15	1.34	1.51	**1.436**	0.046
LaM^2	32	1.46	1.69	**1.571**	0.052	12	1.48	1.63	**1.559**	0.053	15	1.54	1.69	**1.603**	0.046
LaM^3	32	1.37	1.57	**1.455**	0.046	12	1.35	1.52	**1.442**	0.046	15	1.38	1.55	**1.473**	0.054
ACin	32	0.05	0.21	**0.123**	0.038	24	0.04	0.15	**0.096**	0.028	14	0.07	0.17	**0.127**	0.021
LCn	31	0.73	0.94	**0.832**	0.041	8	0.81	0.90	**0.851**	0.036	15	0.78	0.89	**0.835**	0.036
LaCn	31	0.60	0.71	**0.662**	0.038	8	0.64	0.70	**0.675**	0.019	15	0.62	0.71	**0.668**	0.028
RCn	31	1.162	1.343	**1.257**	0.051	8	1.203	1.308	**1.260**	0.036	15	1.152	1.322	**1.251**	0.054
LAt	18	30.5	35.6	**33.70**	1.484	7	31.1	34.8	**33.31**	1.460	13	30.6	35.1	**33.35**	1.509
LPol	18	4.0	4.9	**4.43**	0.240	7	3.9	4.7	**4.40**	0.311	13	4.1	5.1	**4.61**	0.293
LMcV	17	26.5	32.0	**29.69**	1.259	6	27.3	31.7	**29.80**	1.467	13	27.8	32.0	**29.83**	1.370
LMcIV	17	26.4	32.2	**29.64**	1.384	6	27.4	31.2	**29.78**	1.382	13	27.7	31.8	**29.68**	1.242
LMcIII	17	26.8	33.3	**30.71**	1.536	6	28.6	33.1	**31.10**	1.627	13	28.3	32.8	**30.69**	1.470
LMcII	17	24.6	31.2	**28.72**	1.670	6	26.2	31.1	**28.98**	1.876	13	27.1	30.6	**28.79**	1.316
LPVp	17	6.5	8.4	**7.45**	0.504	6	6.8	7.9	**7.40**	0.374	13	6.8	8.1	**7.49**	0.384
LPVm	17	4.9	6.3	**5.62**	0.420	6	4.9	6.1	**5.47**	0.554	12	4.6	6.2	**5.54**	0.456
LPIVp	17	6.9	8.6	**7.79**	0.525	6	7.4	8.4	**7.73**	0.367	13	7.2	8.5	**7.80**	0.453
LPIVm	17	6.2	9.0	**7.46**	0.675	6	6.9	8.4	**7.63**	0.644	13	6.4	8.2	**7.42**	0.546
LPIIIp	17	9.2	11.5	**10.24**	0.593	6	8.6	11.1	**10.08**	0.915	13	9.2	11.5	**10.35**	0.610
LPIIIm	17	8.3	10.1	**9.32**	0.536	6	8.6	10.5	**9.48**	0.725	13	9.0	10.3	**9.71**	0.457
LTib	16	13.4	16.6	**14.78**	0.880	7	13.4	16.5	**14.81**	1.342	13	14.3	15.8	**15.06**	0.493

Tab. 4. Measurements of *Myotis mystacinus* s. l. Southeast-European populations

meas	n	min	max	M	SD	n	min	max	M	SD	n	min	max	M	SD
	Dalmatia [DA] (n = 22)					Ukraine [UA] (n = 34)					Lower Volga Reg. [LV] (n = 16)				
LCr	19	13.32	14.55	**14.040**	0.342	33	13.85	14.90	**14.261**	0.262	15	13.63	14.25	**13.999**	0.186
LCb	20	12.45	13.80	**13.243**	0.356	33	12.25	13.87	**13.442**	0.317	15	12.78	13.70	**13.281**	0.231
LaZ	14	8.00	8.73	**8.431**	0.210	22	8.23	9.07	**8.675**	0.241	12	8.05	9.07	**8.517**	0.279
LaI	22	3.18	3.75	**3.460**	0.120	34	3.38	3.92	**3.611**	0.136	16	3.28	3.72	**3.546**	0.123
LaInf	21	3.18	3.55	**3.355**	0.107	34	3.35	3.85	**3.584**	0.136	16	3.27	3.62	**3.463**	0.092
LaN	20	6.45	7.00	**6.749**	0.145	34	6.65	7.27	**6.979**	0.146	15	6.52	7.18	**6.886**	0.155
ANc	20	4.62	5.02	**4.857**	0.113	34	4.58	5.27	**4.984**	0.151	15	4.62	5.08	**4.881**	0.108
ACr	13	5.63	6.10	**5.915**	0.115	30	5.70	6.33	**6.072**	0.149	13	5.67	6.22	**5.974**	0.154
CC	21	3.05	3.68	**3.445**	0.155	33	3.25	3.87	**3.582**	0.130	16	3.35	3.85	**3.520**	0.144
P^4P^4	21	4.18	4.82	**4.595**	0.175	34	4.52	5.08	**4.768**	0.141	16	4.35	4.92	**4.682**	0.163
M^3M^3	21	5.05	5.70	**5.384**	0.159	33	5.23	5.72	**5.508**	0.135	16	4.97	5.72	**5.453**	0.187
IM^3	22	5.68	6.65	**6.247**	0.224	33	5.95	6.62	**6.278**	0.149	16	5.98	6.48	**6.198**	0.119
CM^3	22	4.75	5.48	**5.167**	0.187	33	4.97	5.50	**5.207**	0.128	16	4.92	5.32	**5.125**	0.094
P^4M^3	22	3.47	3.97	**3.745**	0.121	34	3.66	4.08	**3.844**	0.096	16	3.58	4.03	**3.771**	0.115
M^1M^3	22	2.82	3.21	**3.050**	0.116	34	2.90	3.26	**3.087**	0.080	14	2.95	3.26	**3.056**	0.072
M^2M^3	22	2.20	2.52	**2.366**	0.081	34	2.26	2.51	**2.378**	0.068	16	2.26	2.51	**2.324**	0.060
CP^4	22	2.25	2.60	**2.393**	0.087	33	2.23	2.57	**2.394**	0.095	16	2.23	2.45	**2.339**	0.060
P^3P^3	22	0.64	0.80	**0.724**	0.052	34	0.53	0.78	**0.648**	0.058	16	0.58	0.80	**0.650**	0.063
LP^3	22	0.27	0.38	**0.333**	0.027	34	0.22	0.38	**0.289**	0.035	16	0.25	0.37	**0.297**	0.027
LMd	22	9.32	10.20	**9.822**	0.297	33	9.60	10.43	**10.048**	0.193	16	9.57	10.17	**9.916**	0.195
ACo	20	2.60	2.95	**2.793**	0.096	32	2.60	3.08	**2.856**	0.139	16	2.50	2.93	**2.799**	0.106
IM_3	20	6.10	6.93	**6.620**	0.208	32	6.37	7.08	**6.654**	0.162	16	6.25	6.80	**6.543**	0.149
CM_3	22	5.08	5.92	**5.546**	0.222	33	5.35	5.93	**5.619**	0.131	16	5.28	5.68	**5.492**	0.115
P_4M_3	22	3.71	4.24	**4.049**	0.145	33	3.87	4.29	**4.112**	0.108	16	3.87	4.16	**4.035**	0.085
M_1M_3	22	3.13	3.66	**3.402**	0.130	33	3.21	3.82	**3.463**	0.110	16	3.26	3.50	**3.378**	0.069
CP_4	21	2.09	2.34	**2.206**	0.092	33	2.03	2.42	**2.183**	0.082	16	1.95	2.29	**2.128**	0.079
P_3P_3	22	0.76	0.90	**0.838**	0.041	33	0.66	0.92	**0.788**	0.059	16	0.71	0.86	**0.772**	0.038
LP_3	22	0.30	0.42	**0.361**	0.028	32	0.25	0.40	**0.335**	0.032	16	0.28	0.39	**0.323**	0.029
LaP^4	20	1.10	1.32	**1.220**	0.056	34	1.19	1.40	**1.285**	0.051	16	1.17	1.40	**1.278**	0.058
LaM^1	20	1.29	1.57	**1.393**	0.060	34	1.26	1.57	**1.420**	0.064	16	1.38	1.49	**1.429**	0.039
LaM^2	20	1.46	1.77	**1.579**	0.062	34	1.51	1.70	**1.605**	0.048	16	1.53	1.68	**1.586**	0.046
LaM^3	20	1.32	1.49	**1.415**	0.045	34	1.36	1.57	**1.460**	0.056	16	1.34	1.58	**1.451**	0.067
ACin	22	0.00	0.08	**0.043**	0.018	34	0.00	0.11	**0.042**	0.027	16	0.00	0.09	**0.046**	0.024
LCn	12	0.88	1.02	**0.936**	0.036	33	0.84	1.05	**0.946**	0.051	15	0.86	0.96	**0.911**	0.040
LaCn	12	0.64	0.75	**0.698**	0.033	33	0.63	0.75	**0.690**	0.031	15	0.63	0.73	**0.676**	0.033
RCn	12	1.269	1.400	**1.342**	0.039	33	1.235	1.500	**1.372**	0.068	15	1.262	1.483	**1.350**	0.057
LAt	23	32.2	36.7	**34.95**	1.212	7	33.0	35.6	**34.46**	0.875	14	32.9	35.7	**34.01**	0.894
LPol	22	4.6	5.7	**5.19**	0.292	7	5.1	5.7	**5.39**	0.219	14	5.2	5.8	**5.56**	0.191
LMcV	22	28.6	34.3	**30.86**	1.356	7	28.5	31.3	**30.36**	1.053	14	28.4	32.6	**30.01**	1.124
LMcIV	22	28.6	35.0	**31.21**	1.504	7	28.1	31.5	**30.37**	1.220	14	28.3	31.5	**30.13**	0.912
LMcIII	22	28.8	35.7	**31.88**	1.614	7	29.4	32.4	**31.49**	1.024	14	29.5	33.6	**31.11**	0.973
LMcII	21	27.0	32.7	**29.95**	1.487	7	27.7	31.4	**29.93**	1.280	14	28.3	31.5	**29.64**	1.029
LPVp	22	7.1	8.6	**7.81**	0.398	7	7.3	8.2	**7.94**	0.321	14	7.2	9.0	**7.93**	0.443
LPVm	22	5.1	6.8	**6.13**	0.417	7	6.1	6.6	**6.37**	0.189	14	5.5	7.0	**6.07**	0.432
LPIVp	22	7.4	9.1	**8.18**	0.415	7	7.6	8.7	**7.99**	0.398	14	6.4	8.7	**7.51**	0.503
LPIVm	22	7.1	8.5	**7.76**	0.388	7	7.8	8.7	**8.21**	0.363	14	6.8	9.1	**7.88**	0.539
LPIIIp	22	9.7	11.6	**10.56**	0.458	7	9.4	10.9	**10.01**	0.521	14	9.2	10.8	**9.94**	0.448
LPIIIm	22	9.4	11.8	**10.66**	0.601	7	9.3	10.2	**9.84**	0.336	14	8.7	11.0	**9.67**	0.654
LTib	18	14.9	16.6	**15.71**	0.447	7	15.0	15.9	**15.37**	0.373	14	14.2	15.7	**15.14**	0.416

Tab 5 Measurements of *Myotis mystacinus* s l Ciscaucasian and Caucasian populations

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	Ciscaucasia [CC] (n = 26)					Great Armenia [TC] (n = 31)					Sevan Lake Basin [SB] (n = 17)				
LCr	*25*	12.60	14.45	**13.568**	0.503	*29*	12.73	14.42	**13.597**	0.315	*17*	13.02	14.18	**13.662**	0.313
LCb	*25*	11.95	13.75	**12.877**	0.464	*29*	12.21	13.73	**12.907**	0.300	*17*	12.22	13.32	**12.880**	0.305
LaZ	*15*	7.78	8.83	**8.395**	0.297	*26*	7.67	8.65	**8.267**	0.208	*11*	7.85	8.75	**8.205**	0.289
LaI	*26*	3.15	3.75	**3.453**	0.144	*31*	3.15	3.87	**3.404**	0.153	*17*	3.08	3.52	**3.365**	0.126
LaInf	*26*	3.07	3.63	**3.387**	0.122	*31*	3.11	3.63	**3.358**	0.118	*17*	3.12	3.53	**3.326**	0.112
LaN	*26*	6.12	7.10	**6.719**	0.226	*31*	6.35	6.92	**6.647**	0.154	*17*	6.42	7.13	**6.634**	0.176
ANc	*25*	4.52	5.22	**4.783**	0.188	*29*	4.43	5.17	**4.792**	0.197	*16*	4.47	5.00	**4.792**	0.156
ACr	*24*	5.52	6.46	**5.867**	0.232	*28*	5.40	6.28	**5.87**	0.199	*6*	5.35	6.15	**5.835**	0.296
CC	*26*	3.07	3.60	**3.367**	0.118	*29*	2.95	3.50	**3.300**	0.134	*17*	2.97	3.53	**3.282**	0.144
P^4P^4	*26*	4.10	4.87	**4.568**	0.177	*31*	4.10	4.77	**4.486**	0.140	*17*	4.17	4.58	**4.429**	0.120
M^3M^3	*25*	4.92	5.70	**5.336**	0.200	*31*	4.92	5.52	**5.547**	0.138	*17*	4.83	5.52	**5.211**	0.199
IM^3	*25*	5.55	6.37	**6.056**	0.187	*31*	5.72	6.57	**6.113**	0.160	*17*	5.60	6.28	**5.979**	0.195
CM^3	*26*	4.63	5.42	**5.017**	0.177	*30*	4.87	5.45	**5.124**	0.118	*17*	4.57	5.22	**4.955**	0.165
P^4M^3	*26*	3.45	4.00	**3.702**	0.139	*30*	3.65	4.03	**3.783**	0.093	*17*	3.40	3.95	**3.636**	0.143
M^1M^3	*26*	2.74	3.16	**2.964**	0.115	*30*	2.90	3.24	**3.034**	0.084	*17*	2.79	3.16	**2.932**	0.107
M^1M^2	*26*	2.15	2.49	**2.312**	0.094	*30*	2.18	2.52	**2.344**	0.080	*17*	2.12	2.45	**2.263**	0.094
CP^4	*26*	2.12	2.62	**2.326**	0.120	*28*	2.23	2.59	**2.403**	0.088	*17*	2.14	2.51	**2.299**	0.095
P^2P^3	*26*	0.51	0.82	**0.669**	0.080	*30*	0.59	0.89	**0.702**	0.071	*17*	0.62	0.76	**0.683**	0.042
LP^3	*26*	0.22	0.36	**0.297**	0.039	*30*	0.25	0.41	**0.320**	0.041	*17*	0.23	0.37	**0.300**	0.030
LMd	*25*	9.05	10.18	**9.605**	0.306	*29*	8.95	9.93	**9.580**	0.222	*14*	9.20	9.95	**9.521**	0.226
ACo	*24*	2.45	2.97	**2.719**	0.141	*29*	3.32	3.03	**2.677**	0.128	*14*	2.42	3.02	**2.735**	0.168
IM_3	*25*	5.82	6.70	**6.418**	0.194	*29*	5.93	6.76	**6.514**	0.161	*13*	6.00	6.67	**6.338**	0.224
CM_3	*25*	4.93	5.73	**5.415**	0.154	*28*	5.32	5.80	**5.519**	0.104	*14*	5.03	5.66	**5.370**	0.165
P_4M_3	*25*	3.68	4.26	**3.966**	0.157	*29*	3.76	4.32	**4.045**	0.110	*14*	3.76	4.05	**3.885**	0.091
M_1M_3	*25*	3.08	3.61	**3.329**	0.138	*28*	3.22	3.61	**3.393**	0.086	*14*	3.16	3.37	**3.241**	0.070
CP_4	*25*	1.98	2.32	**2.121**	0.094	*28*	1.92	2.35	**2.147**	0.102	*14*	1.92	2.20	**2.090**	0.080
P_2P_3	*25*	0.68	0.90	**0.781**	0.058	*29*	0.67	0.93	**0.802**	0.053	*14*	0.67	0.86	**0.776**	0.049
LP_3	*25*	0.25	0.40	**0.333**	0.041	*29*	0.29	0.45	**0.351**	0.030	*14*	0.26	0.36	**0.312**	0.027
LaP^4	*26*	1.03	1.37	**1.227**	0.078	*30*	1.13	1.38	**1.235**	0.058	*17*	1.09	1.30	**1.202**	0.058
LaM^1	*26*	1.31	1.48	**1.389**	0.053	*30*	1.28	1.60	**1.391**	0.077	*17*	1.24	1.41	**1.326**	0.050
LaM^2	*26*	1.47	1.68	**1.559**	0.061	*30*	1.46	1.74	**1.573**	0.071	*17*	1.39	1.57	**1.512**	0.044
LaM^3	*26*	1.32	1.61	**1.426**	0.075	*30*	1.30	1.59	**1.442**	0.076	*17*	1.31	1.51	**1.414**	0.057
ACin	*25*	0.03	0.15	**0.081**	0.040	*30*	0.00	0.18	**0.074**	0.044	*17*	0.02	0.11	**0.055**	0.022
LCn	*25*	0.74	0.93	**0.850**	0.052	*29*	0.82	0.96	**0.903**	0.039	*17*	0.78	0.91	**0.864**	0.033
LaCn	*25*	0.57	0.73	**0.640**	0.045	*29*	0.60	0.74	**0.668**	0.037	*17*	0.57	0.69	**0.624**	0.033
RCn	*25*	1.190	1.450	**1.330**	0.061	*29*	1.145	1.508	**1.356**	0.082	*17*	1.227	1.537	**1.388**	0.081
LAt	*7*	33.5	35.9	**34.47**	0.886	*12*	32.2	37.3	**35.12**	1.304	*11*	34.5	37.3	**35.59**	0.824
LPol	*7*	4.7	5.5	**5.11**	0.285	*13*	4.6	5.4	**5.01**	0.210	*11*	5.1	6.2	**5.46**	0.341
LMcV	*7*	30.1	32.1	**31.11**	0.657	*11*	27.8	32.3	**30.99**	1.452	*11*	31.2	35.2	**32.76**	1.097
LMcIV	*7*	30.4	32.9	**31.53**	0.748	*11*	27.1	32.8	**31.16**	1.605	*11*	30.7	35.4	**32.81**	1.275
LMcIII	*7*	31.1	33.8	**32.40**	0.906	*11*	28.6	33.3	**32.07**	1.416	*11*	31.6	35.6	**33.25**	1.031
LMcII	*7*	29.5	31.8	**30.71**	0.821	*11*	25.4	32.4	**30.26**	2.159	*11*	24.5	33.5	**30.69**	2.372
LPVp	*7*	7.5	8.7	**8.23**	0.386	*11*	6.0	8.8	**7.85**	0.795	*11*	7.8	9.3	**8.50**	0.504
LPVm	*7*	5.1	6.8	**5.94**	0.519	*11*	4.6	6.8	**6.06**	0.658	*11*	5.9	7.2	**6.57**	0.372
LPIVp	*7*	7.7	8.8	**8.26**	0.331	*11*	6.9	8.8	**8.10**	0.533	*11*	8.0	9.6	**8.77**	0.516
LPIVm	*7*	6.8	9.1	**7.93**	0.699	*11*	7.1	9.2	**8.07**	0.603	*11*	7.2	9.1	**8.30**	0.598
LPIIIp	*7*	10.1	11.7	**10.64**	0.559	*11*	9.1	11.6	**10.62**	0.804	*11*	10.2	11.9	**11.03**	0.631
LPIIIm	*7*	9.3	10.9	**10.07**	0.665	*11*	9.4	11.6	**10.61**	0.691	*11*	9.2	12.0	**10.86**	0.834
LTib	*7*	14.4	16.2	**15.24**	0.597	*9*	15.8	17.5	**16.54**	0.445	*11*	14.2	17.0	**15.54**	0.874

Tab 6 Measurements of *Myotis mystacinus* s l Northeast-European and West-Turkestan populations

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	N-Baltic Region [BT] (n = 6)					Ural Region [UR] (n = 14)					W-Turkestan [TM] (n = 15)				
LCr	*4*	13.15	13.82	**13.555**	0.286	*13*	12.88	13.73	**13.508**	0.268	*15*	13.02	13.88	**13.481**	0.265
LCb	*4*	12.45	12.95	**12.700**	0.252	*13*	12.15	13.20	**12.907**	0.292	*14*	12.32	13.08	**12.788**	0.211
LaZ	–	–	–	–	–	*9*	8.00	8.38	**8.150**	0.139	*8*	7.80	8.58	**8.143**	0.276
LaI	*5*	3.43	3.62	**3.514**	0.074	*14*	3.35	3.85	**3.580**	0.150	*15*	3.17	3.62	**3.383**	0.135
LaInt	*6*	3.10	3.55	**3.222**	0.164	*14*	3.00	3.52	**3.260**	0.130	*15*	3.12	3.68	**3.389**	0.147
LaN	*3*	6.40	6.73	**6.610**	0.182	*14*	6.53	7.12	**6.734**	0.173	*15*	6.45	6.92	**6.651**	0.140
ANc	*3*	4.58	4.95	**4.767**	0.185	*13*	4.47	4.95	**4.735**	0.156	*15*	4.43	4.93	**4.743**	0.129
ACr	*3*	5.47	5.75	**5.597**	0.142	*11*	5.63	6.02	**5.777**	0.118	*13*	5.58	6.00	**5.795**	0.123
CC	*5*	3.05	3.38	**3.260**	0.126	*14*	3.15	3.42	**3.321**	0.083	*15*	3.12	3.55	**3.384**	0.134
P^4P^4	*6*	4.15	4.43	**4.340**	0.115	*14*	4.32	4.70	**4.458**	0.112	*15*	4.32	4.67	**4.500**	0.087
M^3M^3	*4*	4.87	5.15	**5.050**	0.124	*14*	5.13	5.50	**5.278**	0.108	*13*	5.03	5.33	**5.224**	0.100
IM^3	*5*	5.85	6.37	**6.106**	0.227	*14*	5.83	6.62	**6.151**	0.189	*15*	5.55	6.32	**5.980**	0.186
CM^3	*5*	4.75	5.22	**4.972**	0.194	*14*	4.82	5.25	**5.074**	0.116	*15*	4.74	5.23	**4.946**	0.148
P^4M^3	*6*	3.53	3.92	**3.671**	0.160	*14*	3.55	3.87	**3.686**	0.081	*15*	3.55	3.90	**3.740**	0.085
M^1M^3	*6*	2.84	3.11	**2.939**	0.121	*14*	2.87	3.11	**3.013**	0.069	*15*	2.90	3.16	**3.025**	0.073
M^1M^2	*6*	2.17	2.42	**2.268**	0.107	*14*	2.23	2.43	**2.330**	0.065	*15*	2.26	2.45	**2.311**	0.054
CP^4	*5*	2.26	2.42	**2.331**	0.067	*14*	2.23	2.60	**2.363**	0.108	*15*	2.11	2.38	**2.248**	0.081
P^2P^3	*4*	0.57	0.75	**0.686**	0.084	*14*	0.63	0.84	**0.731**	0.053	*14*	0.56	0.76	**0.676**	0.051
LP^3	*6*	0.27	0.38	**0.321**	0.039	*14*	0.27	0.40	**0.341**	0.034	*12*	0.20	0.33	**0.257**	0.034
LMd	*5*	9.32	9.68	**9.456**	0.183	*14*	9.08	9.98	**9.623**	0.227	*14*	9.20	9.75	**9.474**	0.177
ACo	*5*	2.45	2.83	**2.640**	0.135	*13*	2.37	2.85	**2.658**	0.141	*14*	2.45	2.83	**2.673**	0.109
IM_3	*5*	6.30	6.65	**6.438**	0.154	*14*	6.12	6.85	**6.479**	0.171	*14*	6.18	6.60	**6.383**	0.133
CM_3	*6*	5.28	5.67	**5.450**	0.151	*14*	5.20	5.60	**5.416**	0.115	*14*	5.08	5.58	**5.349**	0.117
P_4M_3	*6*	3.74	4.16	**3.974**	0.148	*14*	3.79	4.21	**3.961**	0.112	*14*	3.90	4.24	**4.015**	0.109
M_1M_3	*6*	3.13	3.45	**3.294**	0.122	*14*	3.16	3.55	**3.346**	0.110	*14*	3.21	3.55	**3.336**	0.092
CP_4	*5*	2.04	2.20	**2.124**	0.060	*14*	2.01	2.34	**2.162**	0.096	*14*	1.73	2.15	**1.992**	0.117
P_2P_3	*5*	0.73	0.96	**0.825**	0.089	*14*	0.75	0.96	**0.862**	0.067	*14*	0.57	0.76	**0.676**	0.051
LP_3	*6*	0.28	0.43	**0.366**	0.054	*14*	0.27	0.44	**0.349**	0.045	*14*	0.25	0.36	**0.308**	0.039
LaP^4	*6*	1.12	1.32	**1.206**	0.076	*14*	1.11	1.26	**1.203**	0.044	*15*	1.12	1.31	**1.216**	0.055
LaM^1	*6*	1.28	1.51	**1.377**	0.086	*14*	1.28	1.42	**1.372**	0.046	*15*	1.32	1.51	**1.395**	0.052
LaM^2	*6*	1.42	1.68	**1.532**	0.090	*14*	1.49	1.61	**1.537**	0.040	*15*	1.49	1.67	**1.564**	0.048
LaM^3	*6*	1.32	1.55	**1.431**	0.081	*14*	1.36	1.54	**1.439**	0.058	*15*	1.30	1.51	**1.412**	0.063
ACm	*6*	0.06	0.15	**0.108**	0.033	*14*	0.05	0.18	**0.120**	0.040	*15*	0.02	0.15	**0.060**	0.034
LCn	*3*	0.79	0.94	**0.866**	0.079	*14*	0.74	0.91	**0.834**	0.050	*14*	0.83	0.95	**0.891**	0.039
LaCn	*3*	0.60	0.72	**0.677**	0.070	*14*	0.61	0.74	**0.669**	0.038	*14*	0.62	0.69	**0.660**	0.023
RCn	*3*	1.203	1.324	**1.281**	0.068	*14*	1.109	1.367	**1.246**	0.079	*14*	1.254	1.467	**1.349**	0.058
LAt	*3*	32.2	33.6	**32.97**	0.709	*10*	31.3	34.5	**32.79**	0.933	*12*	33.2	34.5	**33.65**	0.410
LPol	*3*	4.7	5.2	**4.93**	0.252	*10*	4.7	5.0	**4.89**	0.074	*12*	4.6	5.3	**4.97**	0.227
LMcV	*3*	26.8	28.8	**27.77**	1.002	*10*	28.3	29.8	**28.99**	0.526	*12*	28.5	31.0	**29.83**	0.842
LMcIV	*3*	26.4	28.3	**27.63**	1.069	*10*	28.0	30.0	**28.79**	0.714	*12*	28.6	31.4	**30.13**	0.784
LMcIII	*3*	28.3	29.4	**28.97**	0.586	*10*	29.2	31.3	**29.75**	0.636	*12*	29.4	32.3	**31.03**	0.819
LMcII	*3*	25.7	28.9	**27.33**	1.601	*10*	27.2	30.1	**28.13**	0.898	*12*	27.6	30.8	**29.20**	0.918
LPVp	*3*	6.2	7.2	**6.80**	0.529	*10*	6.9	8.0	**7.30**	0.327	*12*	7.3	8.0	**7.72**	0.221
LPVm	*3*	5.0	5.6	**5.33**	0.306	*10*	4.5	6.1	**5.38**	0.449	*12*	4.8	7.7	**6.43**	0.682
LPIVp	*3*	6.2	7.8	**7.20**	0.872	*10*	6.9	8.3	**7.31**	0.401	*12*	7.1	8.2	**7.71**	0.358
LPIVm	*3*	6.1	8.5	**7.20**	1.212	*10*	6.4	7.8	**7.05**	0.445	*12*	7.0	8.5	**7.76**	0.458
LPIIIp	*3*	8.8	10.1	**9.63**	0.723	*10*	9.1	10.9	**9.89**	0.509	*12*	9.2	10.5	**9.97**	0.345
LPIIIm	*3*	8.3	9.0	**8.53**	0.404	*10*	8.3	9.7	**9.12**	0.426	*12*	8.9	11.8	**9.86**	0.802
LTib	*2*	13.9	14.0	**13.95**	0.071	*10*	13.9	16.5	**14.67**	0.765	*11*	14.9	16.2	**15.51**	0.485

Tab. 7. Measurements of *Myotis mystacinus* s. l.: North-Balkan populations of *M. mystacinus* s. l. and of two newly defined taxa (*M. mystacinus* s. s. and *M. aurascens*)

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	North-Balkans [BL] (n = 93)					BL, *M. mystacinus* s. s. (n = 28)					BL, *M. aurascens* (n = 65)				
LCr	*91*	12.57	14.62	**13.815**	0.448	*26*	12.57	13.85	**13.271**	0.335	*65*	13.37	14.62	**14.035**	0.260
LCb	*89*	11.79	13.85	**13.091**	0.412	*26*	11.79	13.27	**12.612**	0.336	*63*	12.68	13.85	**13.294**	0.241
LaZ	*71*	7.80	9.02	**8.381**	0.268	*19*	7.80	8.73	**8.127**	0.235	*52*	7.95	9.02	**8.476**	0.211
LaI	*93*	3.00	3.71	**3.382**	0.155	*28*	3.00	3.53	**3.264**	0.135	*65*	3.10	3.71	**3.432**	0.132
LaInf	*93*	2.92	3.82	**3.348**	0.175	*28*	2.98	3.76	**3.249**	0.152	*65*	2.92	3.82	**3.388**	0.166
LaN	*93*	6.07	7.18	**6.713**	0.223	*28*	6.07	6.78	**6.499**	0.193	*65*	6.37	7.18	**6.799**	0.167
ANc	*91*	4.38	5.20	**4.813**	0.192	*26*	4.38	5.00	**4.645**	0.155	*65*	4.55	5.20	**4.879**	0.161
ACr	*79*	5.31	6.42	**5.922**	0.241	*26*	5.31	6.27	**5.731**	0.189	*53*	5.60	6.42	**6.017**	0.203
CC	*90*	2.73	3.67	**3.394**	0.167	*26*	2.73	3.52	**3.247**	0.165	*64*	3.08	3.67	**3.454**	0.125
P^4P^4	*91*	3.90	4.97	**4.531**	0.193	*26*	3.90	4.67	**4.399**	0.186	*65*	4.03	4.97	**4.585**	0.168
M^3M^3	*90*	4.75	5.75	**5.343**	0.207	*25*	4.75	5.57	**5.154**	0.209	*65*	5.04	5.75	**5.418**	0.152
IM^3	*92*	5.69	6.60	**6.218**	0.200	*28*	5.69	6.37	**6.023**	0.176	*64*	5.88	6.60	**6.303**	0.141
CM^3	*93*	4.75	5.62	**5.152**	0.170	*28*	4.75	5.33	**4.996**	0.148	*65*	4.80	5.62	**5.217**	0.128
P^4M^3	*93*	3.43	4.11	**3.812**	0.155	*28*	3.43	3.95	**3.695**	0.127	*65*	3.47	4.11	**3.865**	0.137
M^1M^3	*93*	2.84	3.42	**3.105**	0.120	*28*	2.84	3.21	**3.007**	0.091	*65*	2.84	3.34	**3.148**	0.104
M^1M^2	*84*	2.14	2.60	**2.389**	0.103	*26*	2.14	2.45	**2.318**	0.089	*58*	2.15	2.60	**2.423**	0.093
CP^4	*88*	2.21	2.68	**2.432**	0.107	*26*	2.26	2.68	**2.414**	0.113	*62*	2.21	2.65	**2.440**	0.102
P^2P^3	*84*	0.59	0.88	**0.730**	0.063	*26*	0.67	0.88	**0.748**	0.052	*58*	0.59	0.85	**0.723**	0.066
LP^3	*82*	0.21	0.45	**0.330**	0.043	*26*	0.29	0.45	**0.348**	0.034	*56*	0.21	0.40	**0.322**	0.044
LMd	*92*	9.05	10.50	**9.763**	0.322	*28*	9.05	9.92	**9.444**	0.216	*64*	9.13	10.50	**9.912**	0.256
ACo	*92*	2.42	3.12	**2.776**	0.147	*28*	2.42	2.97	**2.650**	0.132	*64*	2.48	3.12	**2.833**	0.116
IM_3	*90*	6.07	7.02	**6.590**	0.194	*28*	6.07	6.82	**6.416**	0.164	*62*	6.27	7.02	**6.670**	0.150
CM_3	*92*	5.09	0.92	**5.574**	0.184	*28*	5.09	5.77	**5.407**	0.161	*64*	5.30	5.92	**5.646**	0.139
P_4M_3	*91*	3.63	4.50	**4.126**	0.171	*28*	3.71	4.24	**4.015**	0.135	*63*	3.63	4.50	**4.179**	0.161
M_1M_3	*92*	3.03	3.74	**3.445**	0.142	*28*	3.11	3.57	**3.348**	0.111	*64*	3.03	3.74	**3.490**	0.132
CP_4	*84*	1.94	2.45	**2.201**	0.098	*26*	1.94	2.40	**2.162**	0.102	*58*	2.01	2.45	**2.218**	0.091
P_2P_3	*82*	0.71	1.04	**0.839**	0.058	*26*	0.71	1.04	**0.863**	0.070	*56*	0.71	0.96	**0.828**	0.048
LP_3	*82*	0.27	0.47	**0.365**	0.038	*26*	0.29	0.47	**0.379**	0.041	*56*	0.27	0.45	**0.359**	0.034
LaP^4	*84*	1.03	1.38	**1.237**	0.076	*26*	1.07	1.38	**1.204**	0.081	*58*	1.03	1.37	**1.252**	0.069
LaM^1	*84*	1.22	1.57	**1.409**	0.067	*26*	1.22	1.53	**1.389**	0.067	*58*	1.22	1.57	**1.419**	0.066
LaM^2	*84*	1.42	1.71	**1.590**	0.060	*26*	1.49	1.70	**1.575**	0.048	*58*	1.42	1.71	**1.599**	0.064
LaM^3	*83*	1.32	1.58	**1.461**	0.064	*25*	1.34	1.53	**1.432**	0.047	*58*	1.32	1.58	**1.474**	0.066
ACin	*81*	0.00	0.19	**0.068**	0.046	*24*	0.04	0.19	**0.118**	0.039	*57*	0.00	0.12	**0.044**	0.027
LCn	*75*	0.73	1.00	**0.869**	0.059	*23*	0.73	0.89	**0.818**	0.042	*52*	0.79	1.00	**0.892**	0.050
LaCn	*75*	0.58	0.75	**0.671**	0.038	*23*	0.58	0.72	**0.646**	0.037	*52*	0.61	0.75	**0.683**	0.033
RCn	*71*	1.113	1.444	**1.297**	0.074	*23*	1.129	1.407	**1.269**	0.068	*51*	1.113	1.444	**1.308**	0.073
LAt	*64*	30.4	36.3	**33.88**	1.384	*25*	30.4	35.6	**32.84**	1.339	*39*	32.9	36.3	**34.61**	0.931
LPol	*64*	3.8	5.7	**4.87**	0.449	*25*	3.8	5.7	**4.55**	0.481	*39*	4.5	5.7	**5.07**	0.280
LMcV	*59*	27.2	33.1	**29.98**	1.272	*21*	27.2	31.4	**29.02**	0.982	*38*	28.2	33.1	**30.55**	1.082
LMcIV	*59*	27.2	33.7	**30.37**	1.334	*21*	27.2	32.1	**29.38**	1.078	*38*	28.3	33.7	**30.94**	1.119
LMcIII	*59*	28.1	34.5	**31.45**	1.467	*21*	28.1	32.8	**30.33**	1.254	*38*	28.9	34.5	**32.11**	1.169
LMcII	*58*	25.3	32.8	**29.79**	1.697	*21*	25.3	31.3	**28.39**	1.592	*37*	28.6	32.8	**30.61**	1.135
LPVp	*59*	6.1	9.1	**7.72**	0.593	*21*	6.1	8.3	**7.32**	0.593	*38*	7.2	9.1	**7.95**	0.458
LPVm	*59*	4.3	7.8	**5.89**	0.694	*21*	4.3	7.1	**5.41**	0.711	*38*	5.4	7.8	**6.17**	0.529
LPIVp	*59*	6.8	9.0	**7.97**	0.510	*21*	6.8	9.0	**7.70**	0.532	*38*	7.2	8.9	**8.13**	0.437
LPIVm	*58*	6.1	9.9	**7.75**	0.761	*21*	6.4	8.3	**7.33**	0.529	*37*	6.1	9.9	**8.01**	0.767
LPIIIp	*59*	9.0	11.6	**10.42**	0.588	*21*	9.0	11.2	**10.10**	0.599	*38*	9.4	11.6	**10.61**	0.495
LPIIIm	*59*	8.1	11.5	**10.21**	0.749	*21*	8.1	11.1	**9.61**	0.743	*38*	9.4	11.5	**10.56**	0.516
Tib	*57*	12.8	17.1	**15.33**	0.992	*20*	12.8	16.8	**14.60**	1.061	*37*	14.1	17.1	**15.74**	0.679

Tab 8 Measurements of *Myotis mystacinus* s l Caucasian populations of newly defined taxa (*M mystacinus caucasicus* ssp n, *M aurascens* and *M nipalensis transcaspicus*)

meas	*n*	min	max	**M**	SD	*n*	min	max	**M**	SD	*n*	min	max	**M**	SD
	CA, *M mystacinus* s s (n = 16)					CA, *M aurascens* (n = 23)					CA, *M nipalensis* (n = 19)				
LCr	14	12.60	13.67	**13.245**	0.383	22	13.50	14.45	**13.915**	0.280	19	12.73	13.82	**13.475**	0.270
LCb	14	11.95	13.07	**12.624**	0.400	22	12.78	13.75	**13.172**	0.285	19	12.21	13.22	**12.793**	0.261
LaZ	10	7.78	8.40	**8.091**	0.185	15	8.22	8.83	**8.509**	0.173	16	7.67	8.56	**8.269**	0.209
LaI	16	3.15	3.60	**3.363**	0.134	23	3.18	3.77	**3.497**	0.137	19	3.22	3.87	**3.403**	0.152
LaInt	16	3.07	3.55	**3.333**	0.120	23	3.22	3.63	**3.413**	0.105	19	3.13	3.63	**3.354**	0.123
LaN	16	6.12	6.96	**6.602**	0.217	23	6.48	7.10	**6.818**	0.143	19	6.35	6.80	**6.595**	0.136
ANc	14	4.52	5.02	**4.685**	0.159	22	4.62	5.22	**4.922**	0.145	19	4.43	5.08	**4.710**	0.168
ACr	15	5.52	6.05	**5.755**	0.176	20	5.73	6.46	**6.013**	0.193	17	5.40	6.15	**5.800**	0.173
CC	16	2.95	3.50	**3.293**	0.150	23	3.13	3.60	**3.381**	0.119	17	3.12	3.50	**3.306**	0.107
P^4P^4	16	4.10	4.72	**4.434**	0.207	23	4.45	4.87	**4.618**	0.121	19	4.35	4.68	**4.489**	0.092
M^3M^3	15	4.92	5.43	**5.207**	0.164	23	5.07	5.70	**5.379**	0.159	19	4.92	5.52	**5.238**	0.144
IM^3	16	5.55	6.37	**6.025**	0.225	22	5.98	6.57	**6.156**	0.127	19	5.72	6.35	**6.066**	0.147
CM^3	16	4.63	5.42	**5.023**	0.217	23	4.90	5.45	**5.099**	0.131	18	4.87	3.35	**5.092**	0.109
P^4M^3	16	3.45	3.87	**3.720**	0.144	23	3.50	4.03	**3.752**	0.126	18	3.65	4.00	**3.763**	0.093
M^1M^3	16	2.84	3.21	**3.023**	0.124	23	2.74	3.24	**2.979**	0.111	18	2.90	3.16	**3.009**	0.072
M^1M^2	16	2.17	2.49	**2.352**	0.111	23	2.15	2.52	**2.322**	0.080	18	2.18	2.51	**2.316**	0.068
CP^4	16	2.12	2.62	**2.384**	0.147	23	2.18	2.57	**2.348**	0.097	16	2.23	2.51	**2.376**	0.083
P^3P^3	16	0.51	0.89	**0.731**	0.099	23	0.57	0.80	**0.664**	0.061	18	0.59	0.78	**0.672**	0.052
LP^3	16	0.22	0.41	**0.331**	0.042	23	0.23	0.38	**0.294**	0.040	18	0.25	0.38	**0.308**	0.035
LMd	15	9.05	9.82	**9.456**	0.240	22	9.25	1.18	**9.767**	0.237	18	8.95	9.82	**9.516**	0.222
ACo	14	2.32	2.82	**2.614**	0.143	22	2.53	2.97	**2.750**	0.111	18	2.48	3.03	**2.697**	0.124
IM_3	15	5.82	6.75	**6.425**	0.247	22	6.25	6.76	**6.525**	0.138	18	5.93	6.72	**6.456**	0.168
CM_3	15	4.93	5.73	**5.443**	0.199	22	5.30	5.80	**5.494**	0.135	17	5.32	5.68	**5.481**	0.092
P_4M_3	15	3.74	4.26	**4.018**	0.178	22	3.68	4.26	**3.983**	0.140	18	3.90	4.32	**4.024**	0.095
M_1M_3	15	3.08	3.58	**3.381**	0.141	22	3.08	3.61	**3.352**	0.121	17	3.21	3.61	**3.366**	0.087
CP_4	15	1.98	2.32	**2.128**	0.118	22	2.00	2.31	**2.152**	0.083	17	1.92	2.35	**2.123**	0.099
P_3P_3	15	0.68	0.93	**0.829**	0.072	22	0.71	0.85	**0.775**	0.039	18	0.67	0.86	**0.785**	0.045
LP_3	15	0.26	0.45	**0.362**	0.041	22	0.25	0.38	**0.324**	0.031	18	0.29	0.40	**0.348**	0.026
LaP^4	16	1.03	1.37	**1.223**	0.094	23	1.13	1.38	**1.244**	0.060	18	1.13	1.30	**1.225**	0.047
LaM^1	16	1.31	1.60	**1.420**	0.083	23	1.31	1.51	**1.397**	0.048	18	1.28	1.48	**1.355**	0.054
LaM^2	16	1.48	1.70	**1.586**	0.076	23	1.47	1.74	**1.575**	0.059	18	1.46	1.70	**1.539**	0.058
LaM^3	16	1.35	1.61	**1.466**	0.079	23	1.32	1.59	**1.430**	0.069	18	1.30	1.59	**1.411**	0.072
ACm	16	0.04	0.15	**0.111**	0.030	22	0.00	0.12	**0.055**	0.027	18	0.00	0.18	**0.071**	0.047
LCn	16	0.74	0.94	**0.852**	0.059	22	0.79	0.95	**0.874**	0.048	17	0.86	0.96	**0.913**	0.032
LaCn	16	0.58	0.74	**0.670**	0.052	22	0.57	0.70	**0.640**	0.035	17	0.58	0.71	**0.662**	0.036
RCn	16	1.145	1.343	**1.275**	0.055	22	1.281	1.458	**1.367**	0.051	17	1.317	1.508	**1.381**	0.069
LAt	3	33.7	35.5	**34.83**	0.987	10	33.5	36.4	**34.94**	1.063	6	32.2	37.3	**34.80**	1.617
LPol	4	4.6	5.0	**4.85**	0.173	10	4.7	5.5	**5.12**	0.239	6	4.8	5.4	**5.05**	0.226
LMcV	3	28.8	31.3	**30.33**	1.343	10	30.1	32.3	**31.32**	0.751	5	27.8	32.3	**30.90**	1.779
LMcIV	3	29.3	31.5	**30.73**	1.242	10	30.4	32.9	**31.67**	0.683	5	27.1	32.8	**30.90**	2.195
LMcIII	3	30.2	33.1	**31.97**	1.550	10	31.1	33.8	**32.43**	0.780	5	28.6	33.3	**31.88**	1.867
LMcII	3	27.1	30.8	**29.57**	2.136	10	29.5	32.4	**30.91**	1.064	5	25.4	31.5	**30.02**	2.591
LPVp	3	7.2	8.1	**7.57**	0.473	10	7.5	8.8	**8.32**	0.365	5	6.0	8.6	**7.60**	0.977
LPVm	3	4.6	6.3	**5.63**	0.907	10	5.1	6.8	**6.06**	0.521	5	5.4	6.7	**6.14**	0.586
LPIVp	3	7.5	8.3	**8.00**	0.436	10	7.7	8.8	**8.35**	0.324	5	6.9	8.5	**7.88**	0.602
LPIVm	3	7.1	8.2	**7.77**	0.586	10	6.8	9.2	**8.08**	0.715	5	7.6	8.8	**8.04**	0.537
LPIIIp	3	9.2	10.9	**10.13**	0.862	10	10.1	11.7	**10.80**	0.527	5	9.1	11.6	**10.58**	0.909
LPIIIm	3	9.7	10.6	**10.23**	0.473	10	9.3	11.6	**10.37**	0.759	5	9.4	11.6	**10.56**	0.838
LTib	2	15.8	16.4	**16.10**	0.424	10	14.4	17.5	**15.74**	0.970	4	16.4	16.7	**16.50**	0.141

Tab 9 Measurements of *Myotis brandtii* Central-European populations

meas	*n*	min	max	**M**	SD	*n*	min	max	**M**	SD	*n*	min	max	**M**	SD
	Austria [AU] (n = 15)					Czech Rep [CZ] (n = 34)					Slovakia [SK] (n = 30)				
LCr	*15*	13.65	14.40	**14.081**	0.244	*32*	13.62	14.60	**14.096**	0.261	*30*	13.50	14.83	**14.201**	0.329
LCb	*15*	12.95	13.88	**13.388**	0.287	*31*	12.83	13.97	**13.432**	0.302	*30*	12.85	14.17	**13.531**	0.311
LaZ	*12*	8.20	8.92	**8.551**	0.199	*21*	8.25	8.92	**8.589**	0.198	*20*	8.26	9.12	**8.651**	0.201
LaI	*15*	3.40	3.75	**3.615**	0.116	*34*	3.34	3.89	**3.658**	0.128	*30*	3.38	3.92	**3.667**	0.128
LaInf	*15*	3.22	3.68	**3.487**	0.138	*34*	3.22	3.80	**3.515**	0.133	*30*	3.12	3.85	**3.529**	0.140
LaN	*15*	6.45	7.25	**6.967**	0.200	*32*	6.35	7.32	**7.009**	0.201	*30*	6.48	7.45	**7.056**	0.197
ANc	*15*	4.55	5.00	**4.761**	0.145	*31*	4.53	4.92	**4.727**	0.101	*30*	4.43	5.13	**4.801**	0.168
ACr	*7*	5.65	6.10	**5.906**	0.154	*28*	5.53	6.02	**5.754**	0.136	*27*	5.53	6.24	**5.838**	0.177
CC	*14*	3.25	3.75	**3.486**	0.137	*30*	3.23	3.63	**3.427**	0.096	*28*	3.10	3.67	**3.437**	0.134
P^{4}P^4	*15*	4.38	4.92	**4.603**	0.171	*34*	4.38	4.92	**4.619**	0.135	*30*	4.38	4.93	**4.702**	0.142
M^{3}M^3	*15*	5.03	5.68	**5.413**	0.167	*33*	5.03	5.63	**5.378**	0.137	*30*	5.10	5.81	**5.476**	0.174
IM^3	*15*	6.25	6.80	**6.504**	0.152	*33*	6.13	6.72	**6.455**	0.138	*29*	6.07	6.78	**6.504**	0.184
CM^3	*14*	5.05	5.50	**5.288**	0.154	*33*	5.07	5.52	**5.282**	0.116	*30*	4.97	5.70	**5.348**	0.169
P^{4}M^3	*15*	3.58	3.92	**3.756**	0.083	*34*	3.63	4.05	**3.869**	0.098	*30*	3.61	4.16	**3.932**	0.131
M^{1}M^3	*15*	2.84	3.18	**3.079**	0.100	*34*	2.90	3.40	**3.183**	0.095	*30*	2.87	3.42	**3.224**	0.114
M^{1}M^2	*15*	2.23	2.52	**2.357**	0.076	*34*	2.23	2.54	**2.427**	0.065	*30*	2.23	2.65	**2.473**	0.083
CP^4	*14*	2.25	2.68	**2.450**	0.111	*33*	2.32	2.72	**2.540**	0.097	*30*	2.49	2.82	**2.613**	0.091
P^{2}P^3	*15*	0.67	0.90	**0.784**	0.059	*34*	0.72	0.95	**0.824**	0.050	*30*	0.66	0.93	**0.833**	0.057
LP^3	*15*	0.30	0.43	**0.374**	0.037	*34*	0.34	0.44	**0.391**	0.027	*29*	0.36	0.45	**0.388**	0.021
LMd	*15*	9.53	10.32	**10.035**	0.239	*33*	9.57	10.72	**10.085**	0.255	*29*	9.63	10.60	**10.133**	0.266
ACo	*15*	2.50	2.95	**2.713**	0.124	*33*	2.52	3.00	**2.766**	0.129	*28*	2.43	3.00	**2.736**	0.141
IM$_3$	*15*	6.52	7.02	**6.776**	0.171	*32*	6.48	7.08	**6.757**	0.126	*29*	6.43	7.20	**6.834**	0.192
CM$_3$	*14*	5.47	6.02	**5.707**	0.155	*33*	5.42	5.85	**5.665**	0.109	*29*	5.38	6.03	**5.742**	0.165
P$_4$M$_3$	*15*	3.84	4.13	**4.007**	0.101	*33*	3.84	4.34	**4.167**	0.097	*29*	4.00	4.58	**4.257**	0.131
M$_1$M$_3$	*15*	3.24	3.47	**3.365**	0.077	*33*	3.21	3.61	**3.504**	0.076	*29*	3.34	3.79	**3.564**	0.103
CP$_4$	*14*	2.06	2.37	**2.247**	0.093	*34*	2.17	2.43	**2.317**	0.082	*28*	2.23	2.59	**2.371**	0.092
P$_2$P$_3$	*14*	0.86	0.96	**0.908**	0.036	*32*	0.85	0.98	**0.915**	0.041	*28*	0.79	1.06	**0.941**	0.058
LP$_3$	*14*	0.38	0.45	**0.409**	0.024	*34*	0.29	0.46	**0.407**	0.042	*29*	0.35	0.49	**0.432**	0.035
LaP^4	*15*	1.13	1.40	**1.210**	0.069	*25*	1.17	1.35	**1.252**	0.048	*30*	1.15	1.35	**1.265**	0.051
LaM^1	*15*	1.34	1.51	**1.435**	0.050	*25*	1.34	1.54	**1.480**	0.049	*30*	1.38	1.61	**1.503**	0.064
LaM^2	*15*	1.49	1.65	**1.579**	0.042	*25*	1.55	1.70	**1.631**	0.040	*30*	1.52	1.76	**1.654**	0.067
LaM^3	*15*	1.36	1.51	**1.445**	0.048	*25*	1.37	1.57	**1.476**	0.044	*30*	1.39	1.62	**1.503**	0.060
ACm	*13*	0.11	0.28	**0.215**	0.044	*32*	0.11	0.29	**0.223**	0.042	*28*	0.15	0.34	**0.236**	0.042
LCn	–	–	–	–	–	*19*	0.72	0.90	**0.837**	0.043	*21*	0.73	0.92	**0.831**	0.047
LaCn	–	–	–	–	–	*19*	0.59	0.76	**0.692**	0.050	*21*	0.65	0.76	**0.698**	0.033
RCn	–	–	–	–	–	*19*	1.056	1.390	**1.212**	0.074	*21*	1.061	1.323	**1.191**	0.059
LAt	*8*	34.6	35.8	**35.24**	0.481	*18*	32.9	35.8	**34.69**	0.826	*24*	32.2	37.1	**34.53**	1.063
LPol	*10*	5.0	5.9	**5.47**	0.306	*18*	4.3	5.4	**4.94**	0.301	*24*	4.3	6.1	**5.11**	0.369
LMcV	*10*	27.7	30.9	**29.64**	1.059	*18*	28.8	31.5	**30.01**	0.753	*24*	27.7	31.7	**29.79**	1.007
LMcIV	*10*	27.8	31.2	**29.82**	1.087	*18*	29.2	31.8	**30.53**	0.709	*24*	28.0	32.2	**30.39**	0.983
LMcIII	*10*	28.6	32.2	**30.90**	1.213	*18*	30.4	33.1	**31.60**	0.774	*24*	29.3	33.4	**31.38**	1.009
LMcII	*10*	25.7	30.0	**28.69**	1.534	*18*	28.0	30.9	**29.24**	0.850	*24*	26.4	30.9	**29.23**	1.168
LPVp	*10*	6.9	8.2	**7.52**	0.397	*18*	6.7	8.2	**7.58**	0.387	*24*	6.9	8.4	**7.57**	0.391
LPVm	*10*	4.2	6.5	**5.55**	0.662	*18*	4.6	7.4	**5.51**	0.605	*24*	3.0	6.5	**5.49**	0.644
LPIVp	*10*	7.0	8.3	**7.71**	0.428	*18*	7.3	8.6	**7.97**	0.351	*24*	7.0	8.7	**7.97**	0.408
LPIVm	*10*	6.3	8.3	**7.00**	0.546	*18*	6.4	7.8	**7.02**	0.412	*24*	6.8	8.1	**7.34**	0.326
LPIIIp	*10*	8.4	10.6	**9.77**	0.729	*18*	9.2	11.3	**9.89**	0.605	*24*	8.7	10.8	**9.69**	0.428
LPIIIm	*10*	7.6	9.6	**8.61**	0.677	*18*	7.9	10.3	**8.91**	0.671	*24*	7.8	9.8	**8.77**	0.480
LTib	*9*	13.5	16.0	**14.33**	0.779	*18*	14.1	16.4	**15.07**	0.635	*23*	14.4	16.4	**14.98**	0.480

Tab. 10. Measurements of *Myotis brandtii*. Southeast-European and North-European populations

meas	*n*	min	max	M	SD	*n*	min	max	M	SD	*n*	min	max	M	SD
	North-Balkans [BL] (n = 10)					Caucasus Mts [CA] (n = 7)					N-Baltic Region [BT] (n = 26)				
LCr	*10*	13.70	14.50	**14.152**	0.251	*7*	13.68	14.10	**13.940**	0.142	*24*	13.85	14.80	**14.381**	0.252
LCb	*10*	12.93	13.73	**13.425**	0.227	*7*	13.20	13.42	**13.317**	0.074	*23*	13.05	14.10	**13.696**	0.257
LaZ	*7*	8.23	8.83	**8.530**	0.205	*6*	8.20	8.70	**8.467**	0.199	*12*	8.42	9.05	**8.739**	0.199
LaI	*10*	3.47	3.82	**3.617**	0.107	*7*	3.40	3.72	**3.616**	0.102	*26*	3.53	3.93	**3.708**	0.097
LaInt	*10*	3.35	3.78	**3.548**	0.137	*7*	3.38	3.67	**3.534**	0.097	*25*	3.43	3.87	**3.620**	0.122
LaN	*10*	6.68	7.05	**6.893**	0.143	*7*	6.80	7.03	**6.891**	0.093	*24*	6.73	7.42	**7.081**	0.161
ANc	*10*	4.50	4.82	**4.649**	0.118	*7*	4.55	4.80	**4.677**	0.100	*23*	4.68	5.08	**4.841**	0.109
ACr	*9*	5.48	5.80	**5.650**	0.108	*7*	5.45	5.72	**5.587**	0.100	*14*	5.68	6.32	**5.947**	0.186
CC	*10*	3.17	3.52	**3.356**	0.115	*7*	3.27	3.52	**3.387**	0.090	*22*	3.30	3.72	**3.516**	0.106
P^4P^4	*10*	4.27	4.75	**4.542**	0.140	*7*	4.37	4.68	**4.503**	0.111	*24*	4.42	4.97	**4.733**	0.123
M^3M^3	*10*	5.02	5.47	**5.259**	0.147	*7*	5.08	5.50	**5.277**	0.161	*25*	5.02	5.82	**5.491**	0.452
IM^3	*10*	6.34	6.68	**6.508**	0.119	*7*	6.23	6.48	**6.359**	0.092	*23*	6.43	6.90	**6.615**	0.128
CM^3	*10*	5.28	5.52	**5.402**	0.076	*7*	5.08	5.32	**5.210**	0.084	*26*	5.20	5.60	**5.385**	0.107
P^4M^3	*10*	3.71	4.00	**3.889**	0.081	*7*	3.42	3.84	**3.632**	0.153	*26*	3.63	3.97	**3.834**	0.096
M^1M^3	*10*	3.00	3.26	**3.153**	0.072	*7*	2.74	3.18	**2.977**	0.164	*25*	3.03	3.32	**3.167**	0.084
M^1M^2	*10*	2.23	2.52	**2.407**	0.080	*7*	2.15	2.42	**2.304**	0.101	*26*	2.28	2.55	**2.401**	0.076
CP^4	*10*	2.51	2.77	**2.644**	0.090	*7*	2.35	2.54	**2.426**	0.060	*26*	2.38	2.63	**2.511**	0.061
P^2P^3	*10*	0.76	0.89	**0.855**	0.036	*7*	0.71	0.82	**0.775**	0.038	*25*	0.75	0.86	**0.798**	0.033
LP^3	*10*	0.37	0.43	**0.407**	0.018	*7*	0.30	0.39	**0.358**	0.028	*26*	0.39	0.48	**0.426**	0.026
LMd	*10*	9.62	10.37	**10.054**	0.252	*7*	9.76	10.27	**9.963**	0.168	*25*	9.92	10.65	**10.294**	0.179
ACo	*10*	2.65	2.90	**2.745**	0.078	*6*	2.58	2.92	**2.758**	0.127	*24*	2.70	3.05	**2.880**	0.086
IM_3	*10*	6.68	6.98	**6.830**	0.099	*7*	6.43	6.88	**6.670**	0.154	*26*	6.60	7.20	**6.894**	0.154
CM_3	*10*	5.62	5.95	**5.759**	0.102	*7*	5.47	5.77	**5.606**	0.107	*26*	5.60	6.07	**5.788**	0.146
P_4M_3	*10*	3.90	4.29	**4.147**	0.104	*7*	3.82	4.02	**3.898**	0.087	*26*	3.84	4.34	**4.133**	0.130
M_1M_3	*10*	3.32	3.58	**3.487**	0.077	*7*	3.16	3.42	**3.308**	0.084	*26*	3.26	3.63	**3.492**	0.100
CP_4	*10*	2.15	2.55	**2.395**	0.143	*7*	2.20	2.38	**2.269**	0.070	*26*	2.21	2.42	**2.315**	0.053
P_2P_3	*10*	0.84	1.02	**0.939**	0.057	*7*	0.85	0.93	**0.890**	0.032	*26*	0.82	1.00	**0.917**	0.039
LP_3	*10*	0.39	0.48	**0.432**	0.036	*7*	0.36	0.45	**0.404**	0.030	*26*	0.39	0.48	**0.426**	0.026
LaP^4	*10*	1.17	1.33	**1.261**	0.058	*7*	1.09	1.26	**1.165**	0.052	*25*	1.09	1.34	**1.231**	0.058
LaM^1	*10*	1.38	1.55	**1.489**	0.054	*7*	1.26	1.42	**1.375**	0.056	*25*	1.36	1.54	**1.455**	0.047
LaM^2	*10*	1.52	1.70	**1.619**	0.052	*7*	1.46	1.57	**1.515**	0.046	*26*	1.52	1.68	**1.604**	0.039
LaM^3	*10*	1.38	1.55	**1.479**	0.045	*7*	1.32	1.44	**1.372**	0.044	*26*	1.33	1.51	**1.440**	0.050
ACm	*10*	0.19	0.33	**0.228**	0.045	*3*	0.20	0.26	**0.230**	0.031	*25*	0.18	0.29	**0.243**	0.030
LCn	*10*	0.80	0.88	**0.834**	0.027	*7*	0.74	0.86	**0.817**	0.039	*24*	0.79	0.91	**0.845**	0.034
LaCn	*10*	0.65	0.72	**0.682**	0.028	*7*	0.63	0.71	**0.661**	0.027	*24*	0.62	0.79	**0.698**	0.037
RCn	*10*	1.118	1.306	**1.224**	0.061	*7*	1.183	1.302	**1.236**	0.050	*24*	1.114	1.356	**1.213**	0.057
LAt	*9*	34.5	35.9	**35.39**	0.542	*3*	34.4	35.7	**35.10**	0.653	*19*	33.8	37.1	**35.42**	0.910
LPol	*9*	4.9	5.7	**5.30**	0.316	*3*	5.2	5.4	**5.30**	0.100	*19*	5.2	6.0	**5.55**	0.206
LMcV	*7*	29.7	31.1	**30.39**	0.453	*3*	30.5	30.8	**30.67**	0.153	*19*	29.3	32.2	**30.67**	0.824
LMcIV	*7*	29.7	31.7	**30.89**	0.784	*3*	31.0	31.5	**31.30**	0.265	*19*	29.5	33.0	**31.30**	1.035
LMcIII	*7*	30.9	33.3	**32.09**	0.799	*3*	31.5	32.5	**32.17**	0.577	*19*	30.5	33.6	**32.12**	0.815
LMcII	*7*	29.0	31.2	**30.26**	0.783	*3*	30.0	30.5	**30.27**	0.252	*19*	27.4	32.4	**30.37**	1.241
LPVp	*7*	7.2	7.9	**7.56**	0.264	*3*	7.3	7.8	**7.50**	0.265	*19*	7.2	8.7	**7.95**	0.361
LPVm	*7*	4.9	5.7	**5.34**	0.251	*3*	5.0	5.4	**5.20**	0.200	*18*	4.8	6.1	**5.51**	0.333
LPIVp	*7*	7.7	8.9	**8.21**	0.438	*3*	7.4	8.1	**7.67**	0.379	*19*	7.1	9.0	**8.25**	0.488
LPIVm	*7*	6.3	8.1	**7.34**	0.591	*3*	6.1	6.9	**6.60**	0.436	*19*	6.5	9.2	**7.45**	0.610
LPIIIp	*7*	9.6	10.7	**10.13**	0.415	*3*	9.4	9.5	**9.43**	0.058	*19*	9.3	10.9	**10.05**	0.490
LPIIIm	*7*	8.3	9.4	**8.80**	0.424	*3*	8.6	9.6	**8.93**	0.577	*19*	7.8	10.0	**8.99**	0.580
LTib	*6*	14.5	16.4	**15.63**	0.677	*3*	13.8	15.3	**14.50**	0.755	*14*	13.7	16.3	**15.09**	0.934

Tab. 11. Measurements of *Myotis brandtii* (East-European population), *M. ikonnikovi* (E-Siberian and Far Eastern population) and *M. nipalensis* (East-Turkestan population, type series of *M. n. przewalskii* Bobrinskoj, 1926)

meas	n	min	max	M	SD	n	min	max	M	SD	n	min	max	M	SD
	NE Russia [RU] (n = 18)					*M. ikonnikovi* [iko] (n = 29)					*M. nipalensis* [ET] (n = 4)				
LCr	17	13.70	14.42	**14.102**	0.230	27	12.07	13.25	**12.718**	0.322	–	–	–	–	–
LCb	17	13.17	14.07	**13.485**	0.272	26	11.42	12.62	**12.152**	0.304	1	–	–	**13.450**	–
LaZ	11	8.40	8.80	**8.614**	0.137	16	7.25	8.03	**7.756**	0.200	–	–	–	–	–
LaI	18	3.38	3.82	**3.680**	0.102	27	3.15	3.52	**3.308**	0.096	4	3.10	3.38	**3.300**	0.134
LaInt	18	3.27	3.75	**3.556**	0.123	27	2.96	3.40	**3.188**	0.109	4	3.43	3.68	**3.600**	0.116
LaN	18	6.80	7.32	**7.004**	0.155	26	6.10	6.58	**3.350**	0.117	4	6.50	6.77	**6.645**	0.127
ANc	17	4.56	5.00	**4.828**	0.119	25	4.40	4.87	**4.629**	0.142	2	4.88	4.90	**4.890**	0.014
ACr	14	5.55	6.00	**5.806**	0.105	25	5.25	6.12	**5.688**	0.217	2	5.75	6.12	**5.935**	0.262
CC	18	3.25	3.57	**3.439**	0.084	25	3.02	3.50	**3.288**	0.141	4	3.42	3.52	**3.465**	0.042
P^{4}P^4	18	4.38	4.72	**4.578**	0.101	27	3.87	4.47	**4.226**	0.170	4	4.52	4.72	**4.588**	0.092
M^{3}M^3	18	5.10	5.62	**5.404**	0.121	28	4.61	5.17	**4.930**	0.162	4	5.20	5.62	**5.450**	0.192
IM^3	17	6.12	6.72	**6.414**	0.159	28	5.47	6.02	**5.797**	0.145	3	6.12	6.27	**6.197**	0.075
CM^3	18	5.05	5.52	**5.259**	0.122	28	4.57	5.03	**4.822**	0.109	4	5.15	5.25	**5.208**	0.051
P^{4}M^3	18	3.58	3.92	**3.727**	0.096	29	3.32	3.66	**3.457**	0.082	4	3.84	4.11	**3.974**	0.110
M^{1}M^3	18	2.92	3.21	**3.070**	0.080	29	2.68	3.00	**2.855**	0.077	4	3.18	3.24	**3.204**	0.025
M^{1}M^2	18	2.26	2.51	**2.347**	0.064	29	2.07	2.38	**2.223**	0.069	4	2.45	2.51	**2.469**	0.030
CP^4	18	2.38	2.63	**2.491**	0.073	28	2.11	2.48	**2.292**	0.051	4	2.21	2.48	**2.322**	0.124
P^{3}P^1	17	0.73	0.86	**0.798**	0.039	29	0.65	0.88	**0.768**	0.051	4	0.38	0.57	**0.497**	0.089
LP^3	18	0.31	0.43	**0.375**	0.031	29	0.30	0.42	**0.355**	0.030	4	0.19	0.25	**0.217**	0.034
LMd	17	9.65	10.58	**10.098**	0.238	26	8.62	9.50	**9.043**	0.234	4	9.70	9.90	**9.808**	0.087
ACo	17	2.57	3.07	**2.821**	0.149	27	4.43	2.72	**2.559**	0.077	4	2.68	2.88	**2.773**	0.083
IM$_3$	17	6.50	7.10	**6.759**	0.132	27	5.87	6.43	**6.176**	0.147	4	6.32	6.65	**6.510**	0.154
CM$_3$	17	5.42	5.92	**5.651**	0.122	28	4.63	5.37	**5.166**	0.156	4	5.43	5.52	**5.480**	0.039
P$_4$M$_3$	17	3.82	4.26	**4.011**	0.116	28	3.53	3.95	**3.772**	0.105	4	4.05	4.24	**4.171**	0.082
M$_1$M$_3$	17	3.21	3.55	**3.398**	0.091	28	3.00	3.37	**3.196**	0.090	4	3.29	3.50	**3.421**	0.091
CP$_4$	17	2.14	2.45	**2.281**	0.100	28	1.81	2.20	**2.047**	0.100	4	1.92	2.01	**1.958**	0.046
P$_5$P$_3$	17	0.84	0.97	**0.909**	0.041	28	0.76	0.95	**0.866**	0.040	4	0.55	0.65	**0.592**	0.043
LP$_3$	17	0.27	0.48	**0.414**	0.043	28	0.36	0.46	**0.389**	0.030	4	0.20	0.27	**0.241**	0.031
LaP^4	18	1.07	1.30	**1.205**	0.063	29	0.96	1.22	**1.112**	0.066	4	1.17	1.28	**1.212**	0.047
LaM^1	18	1.30	1.49	**1.402**	0.058	29	1.17	1.40	**1.292**	0.055	4	1.38	1.44	**1.401**	0.025
LaM^2	18	1.49	1.62	**1.563**	0.042	29	1.31	1.59	**1.474**	0.057	4	1.63	1.68	**1.665**	0.021
LaM^3	18	1.24	1.53	**1.414**	0.058	29	1.28	1.51	**1.372**	0.053	4	1.40	1.59	**1.487**	0.082
ACin	16	0.15	0.33	**0.233**	0.050	29	0.04	0.16	**0.099**	0.038	4	0.00	0.00	**0.000**	0.000
LCn	16	0.78	0.91	**0.842**	0.038	25	0.70	0.87	**0.802**	0.044	4	0.92	1.01	**0.969**	0.039
LaCn	16	0.65	0.76	**0.689**	0.034	25	0.58	0.74	**0.655**	0.041	4	0.62	0.67	**0.644**	0.025
RCn	16	1.096	1.318	**1.223**	0.057	25	1.141	1.323	**1.226**	0.051	4	1.444	1.583	**1.505**	0.058
LAt	11	33.5	36.7	**35.19**	0.850	20	29.4	33.5	**31.70**	1.285	4	34.6	35.3	**35.00**	0.316
LPol	11	5.0	6.3	**5.53**	0.405	22	3.8	4.7	**4.32**	0.220	4	4.9	5.4	**5.10**	0.216
LMcV	12	29.6	31.4	**30.60**	0.559	21	26.0	30.5	**28.30**	1.101	4	30.6	31.4	**31.00**	0.337
LMcIV	12	28.0	32.2	**30.72**	1.037	21	26.1	31.2	**28.91**	1.250	4	31.2	32.4	**31.73**	0.538
LMcIII	12	30.4	33.0	**31.88**	0.812	20	27.2	31.9	**29.86**	1.082	4	32.7	33.4	**33.08**	0.377
LMcII	12	28.7	31.9	**30.16**	1.004	21	25.6	30.4	**28.39**	1.159	4	30.3	31.8	**31.15**	0.635
LPVp	12	7.5	8.3	**7.91**	0.261	21	6.5	8.0	**7.29**	0.442	4	7.5	8.7	**8.03**	0.499
LPVm	12	3.6	6.6	**5.33**	0.824	21	4.3	6.3	**5.22**	0.533	4	5.5	6.4	**5.98**	0.377
LPIVp	12	7.7	8.6	**8.13**	0.253	21	6.6	8.1	**7.35**	0.409	4	7.9	8.6	**8.30**	0.294
LPIVm	12	5.4	7.9	**7.03**	0.672	21	5.0	7.8	**6.69**	0.592	4	7.2	8.3	**7.70**	0.497
LPIIIp	12	9.6	10.9	**10.07**	0.347	21	8.3	10.3	**9.40**	0.521	4	10.5	11.0	**10.73**	0.206
LPIIIm	12	8.1	10.1	**9.06**	0.545	21	7.3	10.2	**9.26**	0.601	4	9.6	10.7	**10.28**	0.499
LTib	10	14.2	16.0	**14.79**	0.551	21	12.2	16.2	**14.00**	0.952	4	13.0	15.6	**14.88**	1.253

Acta Soc. Zool. Bohem. 64: 399–401, 2000
ISSN 1211-376X

Metajapyx braueri (Hexapoda: Japygina: Japygidae) in Prague, Bohemia

Karel HŮRKA & Milan ŘEZÁČ

Department of Zoology, Charles University, Viničná 7, CZ–128 44 Praha 2, Czech Republic;
e-mail: hurka@natur.cuni.cz, rezac@natur.cuni.cz

Received November 5, 2000; accepted December 4, 2000
Published December 29, 2000

Abstract. *Metajapyx braueri* (Verhoeff, 1904) was found in an abandoned garden situated on south-facing slope in Praha-Smíchov (50° 05' N, 14° 25' E). This finding shows that the species, native in the biogeographical Pannonian province, is able to survive at warm localities outside its primary area of distribution, with an annual average temperature of 8 to 10 °C.

Distribution, Japygina, Japygidae, *Metajapyx braueri*, Czech Republic

INTRODUCTION

The first finding of Japygina in Bohemia, was *Catajapyx aquilonaris* (Silvestri, 1929), established by Uzel in 1923 in Vinoř, now the suburb of Prague, followed by Roubal (Praha-Střešovice, 1942) and other collectors (Řevnice, several localities in Prague) (Paclt 1956a). Paclt (1956b) considered the isolated occurrence of Japygina in Prague and surroundings as not autochthonous, caused by the garden and/or agricultural activities of man.

In October 1999 and repeatedly in November 2000, the junior author found in the uncared-for part of a garden in Praha-Smíchov several specimens of Japygidae, determined by the senior author as *Metajapyx braueri*.

RESULTS

Metajapyx was described by Silvestri 1932 as subgenus of *Japyx* Haliday, 1865. In 1948 Silvestri raised the taxon to the genus level and provided the diagnosis. Almost 30 species from western, central and southern Europe and from the North Africa were included in the genus. *Metajapyx leruthi* Silvestri, 1948 (in Belgium and Germany) and *Metajapyx braueri* (Verhoeff, 1904) are the northern most distributed species of the genus.

Metajapyx braueri (Verhoeff, 1904)

The first specimen (adult female, in collectio Hůrka) was sampled in October 1999. This specimen, and one other which was not sampled, were found in a leaf litter under shrubs (*Sambucus nigra* with *Urtica dioica*) in the abandoned part of a sloped garden of the Station of Young Scientists in Praha-Smíchov, between streets Drtinova and Holečkova (code of mapping square 5952)*, and once more on November 3, 2000, under stones (adult male, juvenile specimen, in coll. Hůrka). The garden lies on the territory of the former farmstead Kanclířka. In the last 160 years, the sloped plot was planted with a vineyard, an orchard, a park and gardens Consequently, the introduction of japygids with the soil and seedlings was possible and probable

---

* For details see Pruner & Mika (1996)

The species was described (as *Japyx Braueri*) from Hungary, based on one female found under stone near the western edge of the Lake Neusiedler See (Verhoeff 1904) From Moravia, it was first recorded by Kratochvíl (1944) from the vicinity of Lednice (code of mapping square 7266), on a meadow near Gloriett, in 1936 (leg J Kratochvíl) In Slovakia, it was found near Tekovské Lužany (code of mapping square 7977) (7 vi –3 vii 1924, 3 specimens, leg E Dudich) and described by Stach (1929) as *Japyx serratus* (definitively synonymized by Paclt 1956a) In his monographic paper on Diplura of Czechoslovakia, Rusek (1964) confirms the distribution of *Metajapyx braueri* in southern Moravia and in southern Slovakia

According to Pagés (1978) the species is distributed in Moravia, Slovakia, Hungary, Austria (most localities), Slovenia (Postojna – as *Japyx sinuosus* Tuxen, 1930, synonymized by Silvestri 1948), Croatia (Istria) and northern Italy (a cave near Brescia), in lowlands and valleys up to the elevation of 500 m, as clearly demonstrates the map (Fig 1)

The isolated Prague population is far from the northern boundary of the continuous area of species distribution about 200 to 230 km in a beeline It survives in the mentioned locality evidently thanks to the warm urban climate of Prague with the annual average temperature fluctuating in the last 50 years between 7 9 and 9 9 °C (Němec & Ložek 1997)

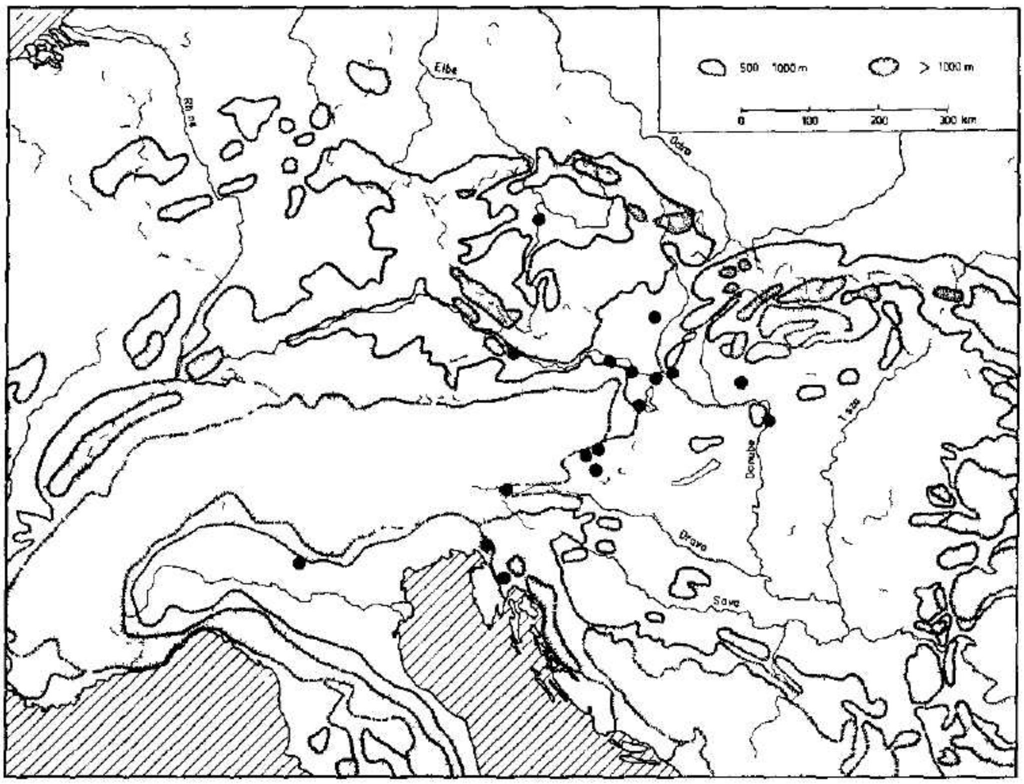


Fig 1 Map of the known localities of *Metajapyx braueri* (Verhoeff)

Acknowledgement

The senior author acknowledges the support of his study by the Research Project of the Ministry of Education of the Czech Republic No. J 13/98113130004.

REFERENCES

Kratochvíl J. 1944: [To the knowledge of the Central-European Japygidae]. *Folia Entomol.* 7: 3–4 (In Czech).

Němec J. & Ložek V. 1997: *Chráněná území ČR 2, Praha [Protected areas of the Czech Republic 2, Praha].* Praha: Agentura ochrany přírody a krajiny ČR, 154 pp.

Paclt J. 1956a: [Diplura of Slovakia and the boundary territories]. *Biol. Práce* **2** (6): 1–25 (In Slovak, Germ., Russ. Summ.).

Paclt J. 1956b: Die Deutung der Prager Funde von Catajapyx (Diplura). *Acta Faun. Entomol. Mus. Natl. Pragae* 1: 27–29.

Pagés J. 1978: Dicellurata Genavensia V. Espèces d'Europe et du bassin méditerranéen. N° 1. *Rev. Suisse Zool.* **85**: 31–46.

Pruner L. & Mika P. 1996: List of settlements in the Czech Republic with associated map field codes for faunistic grid mapping system. *Klapalekiana* **32** (Suppl.): 1–115 (In Czech, Engl. Summary).

Rusek J. 1964: Über die Diplura (Apterygota) der Tschechoslowakei. *Acta Soc. Zool. Bohemoslov.* **28**: 134–154.

Silvestri F. 1932: Nuovi contributi alla conoscenza della fauna delle isole italiane dell'Egeo II. Thysanura-Entotropha (Insecta). *Boll. Labor. Zool. Agr. Portici* **27**: 61–111.

Silvestri F. 1948. Japyginae (Japygidae, Insecta Diplura) della fauna italiana finora note. *Boll. Labor. Entomol. Agr. Portici* **8**: 236–296.

Stach J. 1929: Eine mitteleuropäische Japyx-Art (Apterygogenea). *Annls Mus. Zool. Polon.* **8**: 54–58.

Tuxen S. L. 1930: Einige Apterygoten aus Südeuropa nebst Beschreibung zwei neuer Arten von Thysanura. *Entomol. Meded.* **17**: 219–227.

Verhoeff K. W. 1904: Zur vergleichenden Morphologie und Systematik der Japygiden. *Arch. Naturg.* **70**: 63–114.

Acta Soc Zool Bohem **64** 402, 2000
ISSN 1211-376X

BOOK REVIEW

MEHLHORN H & PIEKARSKI G **Grundriss der Parasitenkunde. Parasiten des Menschen und der Nutztiere** Fifth updated and extended edition Gustav Fischer Verlag, Stuttgart, 1998 XI+516 pages Format 125×190 mm Soft cover Price DME 39 80 ISBN 3-437-25830-3

The first of the authors is professor at the department of zoomorphology, cell biology and parasitology of the Heinrich Heine University in Dusseldorf The second author is the late German parasitologist of a world reputation A favorable acceptance of this book and the flood of new information have led to preparation of new editions Since the first edition in 1981 – for review see *Folia parasitologica* (Prague), 29, 1982, pp 279–280 – *this fifth edition has became extended from 268 to 516 pages This publication demonstrates the extraordinary* creative capability of professor Mehlhorn He acted as author, coauthor or editor of numerous monographs on medical and veterinary parasitology, zoology and protozoology

Two initial chapters provide insights into the phenomena of parasitism and into basic terms, including biological characterizations of parasites, evasion mechanisms, pathogenicity, antibody tests and molecular diagnostics Further on, presented are overviews of systematic classification of protozoans, helminths and arthropods in humans and domestic animals Subsequent text is organized into three parts

Part A is devoted to **Protozoa/Protista** The author gives attention to the intervention of genetics and molecular biology in the taxonomy of protozoans while analyzing of the classification schemes of Cavalier-Smith *Corliss, Hausmann & Hulsmann, and others Nevertheless, traditional classification scheme of Levine et al (1980)* embracing the Sarcomastigophora and the six other phyla is introduced here Actual informations on trichomonads and kinetoplastids, amoebae, apicomplexans, malaria, leishmaniae and other protozoan parasites are looked at

Part B deals with the **helminths** – the situation in taxonomical classification involves here choice between a traditional system and recent phylogenetical approaches while presenting non traditional assemblages (taxa) as are the Neodermata and Cercomeromorphae In this part outlined are morphological aspects and life cycles of flatworms, tapeworms, acanthocephalans, nematodes, tongue worms and annelids with particular reference to species of medical interest

***Part C** is concerned with **arthropods** - in an overview of taxa embracing parasitic species a traditional* classification scheme will be satisfactory Described here are the chelicerates including parasitic mites and ticks, parasitic insects and crustaceans

Particular taxa of parasitic organisms are examined here with reference to the morphology and biology, immunobiology, pathogenic effects upon host organisms, clinical signs, laboratory diagnosis and chemotherapy Moreover, discussed are harmful influences of parasitic arthropods and their vectorial activities Illustrations consist of 184 line drawings of micro- and macroscopic structures and electron microphotographs Stereoscans offer most instructive – non traditional aspects of parasitic organisms Original schematic life cycle drawings are of particular didactic value In addition, there are 19 tables summarizing important species of trypanosomes, *leishmaniae, sarcocysts, digenean trematodes, parasitic nematodes and mites, dipterans causing myiases, and more* An appendix offers control questions for examinations This pocket-sized publication presents a most informative companion to the classical textbooks of parasitology and covers recent advances in the field

Jindrich Jira

Acta Soc. Zool Bohem 64· 403–417, 2000
ISSN 1211-376X

Revisional notes on the Palaearctic *Formicomus* (Coleoptera: Anthicidae)

Zbyněk KEJVAL

Muzeum Chodska, CZ–344 01 Domažlice, Czech Republic, e-mail: kejval@email cz

Received March 27, 2000, accepted December 4, 2000
Published December 29, 2000

Abstract In the present paper *Formicomus amaenus* LaFerté-Sénectère, 1849 and *F. parallelus* Marseul, 1879 are redescribed and three new species, *F. bukharensis* sp. n. (Uzbekistan, Kazakhstan), *F. jelineki* sp. n. (Iran) and *F. persicus* sp. n. (Iran), are described. The following new synonymies are proposed *Formicomus amaenus* La Ferté-Sénectère, 1849 (= *F. mellyi* Pic, 1894 syn. n.); *F. nadari* Pic, 1893 (= *F. sphinx* Krekich-Strassoldo, 1919 syn. n.) The lectotypes for *F. parallelus* Marseul, 1879, *F. nadari* Pic, 1893 and *F. sphinx* Krekich-Strassoldo, 1919 are designated.

Taxonomy, redescription, new species, new synonymy, lectotype designation, Coleoptera, Anthicidae, *Formicomus*, Palaearctic region

INTRODUCTION

Formicomus La Ferté-Sénectère, 1849 is a conspicuous genus, easily distinguishable within Palaearctic Anthicidae. In spite of this fact, the Palaearctic fauna of this genus has never been completely revised and most of its members remain poorly known until now. The present paper contains a part of results obtained in the framework of gradual review of the genus.

MATERIAL AND METHODS

Through the text, the following abbreviations are used (in round brackets) BMNH – British Natural History Museum, London, IRSN – Institute Royal des Sciences naturelles, Brussels, KMVC – Muzeum východních Čech, Hradec Králové, MNHN – Museum national d'Histoire naturelle, Paris; NHMW – Naturhistorisches Museum, Wien, NMPC – Národní Museum, Praha, ZHMB – Zoologisches Museum an der Humboldt Universität, Berlin; CKD – collection Zbyněk Kejval, Domažlice; CUP – collection Gerhard Uhmann, Pressath

Author's comments on the type material are found in square brackets Exact label data are quoted in the type specimens only Separate labels are indicated by slashes (\).

TAXONOMY

Formicomus amaenus La Ferté-Sénectère, 1849
(Figs 1, 2)

Formicomus amoenus [sic!, see errata] La Ferté-Sénectère, 1849a 12, 1849b. 81
Formicomus vosseleri Hille, 1977 198.
Formicomus mellyi Pic, 1894 64, **syn. n.**

REDESCRIPTION (male; see Hille, 1977 for the figures of male characters). Colouration of body variable, *ranging from unicoloured brown-black, with very slight greenish reflection on elytra,* to bicoloured, largely rufous-brown, with posterior two thirds of elytra (behind transverse band of setae) brown-black; antennae and maxillar palpi rufous, antennae somewhat darkened distally; legs rufous to dark brown, tibia, tarsi and narrowed, proximal portion of femora usually somewhat paler.

Head 1.2 times as long as wide, rounded posteriorly (posterior arch widely parabolic); tempora narrowing close behind eyes towards base; hind temporal angles entirely obsolete. Eyes medium, at most moderately convex, not protruding from lateral outlines of head. Neck short, clearly differentiated from head. Dorsal surface of head distinctly punctured and finely longitudinally corrugated. Pubescence composed of short decumbent and few erect, pale setae.

Pronotum 1.4 times as long as wide, narrower than head including eyes, rounded and convex in front, distinctly impressed laterally and at most flattened (not impressed) dorsally in posterior half. Sculpture, punctation and pubescence of dorsal surface similar to that of head, corrugation in anterior half becoming gradually less distinct towards lateral sides, wrinkles mostly longitudinal, only those before base are directed more or less transversely; lateral sides in anterior half only sparsely punctured, especially ventro-laterally, smooth and glossy close before latero-basal impressions; bottom of latero-basal impressions with several short, fine wrinkles and the area behind impressions rugose. Pubescence similar to that of head, with a few short, erect setae anteriorly.

Elytra 1.8 times as long as wide; elytral humeri moderately angulate; hind membranous wings well developed; postscutellar impression moderate. Surface of elytra more sparsely punctured and pubescent than on forebody; ordinary setigerous punctures (Fig. 2), bearing pale decumbent to semierect setae, with two minute impressions posteriorly; punctures at postscutellar impression (Fig. 1) much more densely spaced, nearly contiguous, bearing thicker, whitish, decumbent setae and thus forming rather distinct transverse band, interrupted medially and becoming sparser towards lateral margins (at sloping sides of elytra); ordinary punctures more densely, evenly spaced behind transverse band and somewhat sparser at base; interspaces among setigerous punctures smooth and rather glossy.

Both mesosternum and metasternum simply shaped.

Antennae reaching to elytral humeri; segment I 1.9 times as long as wide; distal segments moderately enlarged and flattened, distinctly longer than wide, segment X 1.4 times as long as wide, segment XI twice as long as wide, 1.3 times as long as the segment X.

All femora distinctly clavate; all tarsi shorter than tibia; the penultimate segment of all tarsi somewhat flattened apically, with the terminal segment implanted at its mid-length dorsally, similarly as in Fig. 30; front legs modified; profemora with long, slim process, bluntly rounded and armed with short, stiff setae apically; protibia with two distinct protrusions at about mid-length.

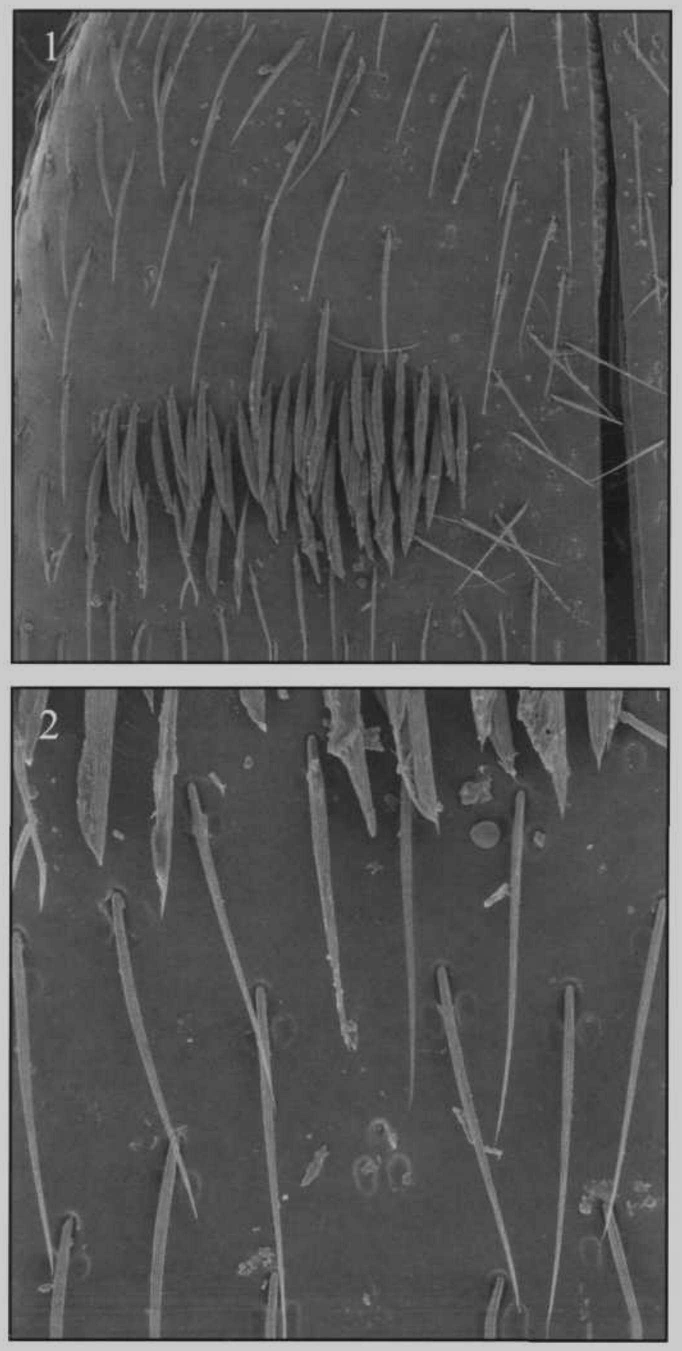
Sternite VII with short medial process, rounded apically and bearing numerous longer, stiff setae along apical margin. Tergite VII simply shaped, with posterior margin rounded and slightly produced apically. Sternite VIII with a pair of curved prongs; each prong, except for shorter pubescence on its medial surface, with long, clustered setae latero-basally. Tergite VIII composed of two paired plates, narrowly connected medially. Aedeagus with apical portion of tegmen distinctly shorter, 0.4 times as long as the basal portion; apex of tegmen narrowed and simply bilobed; median lobe of aedeagus membranous, strengthened by straight, sclerotized apodeme.

SEXUAL DIMORPHISM. Female externally identical with male, but differs by the simple front legs and by the simply shaped abdominal segments VII,VIII.

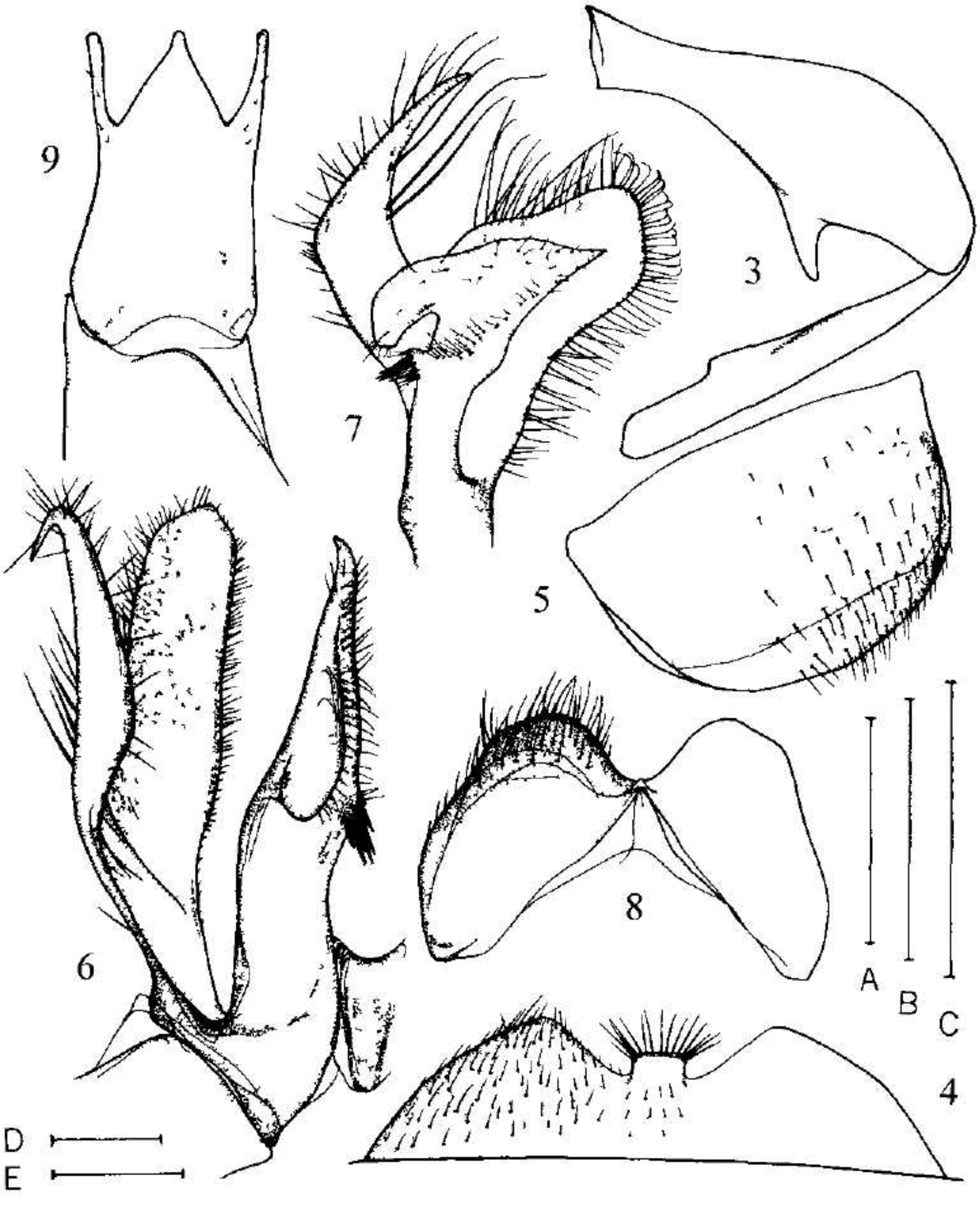
LENGTH. 3.3–3.7 mm.

TYPE MATERIAL EXAMINED. *F. amaenus* – Holotype, female (MNHN)[*mounted on small triangular label*]: "Egypt [handwritten, partly illegible] \ MUSÉUM PARIS 1962 COLL. R. OBERTHUR La Ferté \ TYPE [red label, printed] \ Carteromerus amaenus (Klug) mihi h. in Aegypto d. Klug [handwritten label, pinned separately]". *F. mellyi* – Holotype, female (MNHN)[mounted on small triangular label]: "Egypte [handwritten] \ type [yellowish label, handwritten] \ TYPE [red label, printed] \ MUSÉUM PARIS 1958 COLL. M. PIC \ Mellyi Pic [handwritten]".

ADDITIONAL SPECIMENS EXAMINED. 1 male, 3 females (MNHN, coll. Pic), "Egypte"; 1 male (CKD), Sudan, Hudeiba, 30 km S of Atbara, 15.iii.1978, J. Bremer leg.; 2 males, 3 females (CKD), Sudan, Khartoum, 19.viii.1966, P. Štys leg.



Figs 1, 2. *Formicomus amaenus* LaFerté-Sénectère: 1 – basal third of elytra; 2 – detail of punctation of elytra.



Figs 3–9. *Formicomus bukharensis* sp. n. (male): 3 – front leg, 4 – sternite VII, 5 – tergite VII, 6 – sternite VIII (half), dorsal aspect, 7 – the same, lateral aspect, 8 – tergite VIII, 9 – apical portion of tegmen of aedeagus. Scale (0.5 mm): A – 5, B – 3, 4, C – 8; (0.1 mm): D – 7, 9, E – 6

Distribution. So far known from Egypt, Ethiopia (Pic 1907, 1939) and Sudan (Hille 1977). Records from Saudi Arabia and Yemen by Uhmann (1985, 1998) are based on misidentified specimens of *F. panelii* Hille, 1977.

Remarks. The examined female holotypes of *F. amaenus* and *F. mellyi* share all important morphological characters, including rather typical punctation and pubescence of elytra and corrugation of head and pronotum. Since combination of these characters is rather scarse within the whole genus and, moreover, the additionally examined males fully agree in the male characters, *F mellyi* is regarded as junior synonym of *F. amaenus*.

Based on the specimens from "Askeiht" in north Sudan (near border with Egypt), compared with the identified specimens of the Pic's collection from Ethiopia, Hille (1977) briefly described and figured *F. vosseleri* Pic, 1913 (originally described from Tanzania). Considering the figures of the male characters given by Hille, *F. vosseleri* appears to be identical with *F. amaenus*, however this opinion has to be confirmed by the examination of the female holotype (deposited in ZHMB) along with more extensive material from Tanzania, which was not available for the present study.

Formicomus nadari **Pic, 1893**

(Fig. 30)

Formicomus nadari Pic, 1893: 175

Formicomus sphinx Krekich-Strassoldo, 1919: 171, figs. 6, 7, **syn. n.**

Diagnosis. Having similar colouration (yellowish transverse band at base of elytra) and body-form, *F nadari* at first sight resembles *F. pedestris* (Rossi, 1790) and *F. nemrod* LaFerté-Sénectère, 1849. It can be easily distinguished from both latter species, without dissection of male specimen, by the apically flattened penultimate segment of tarsi (especially metatarsi), with terminal segment implanted at its mid-length dorsally (cf. Figs 29, 30). On the other hand, I can not see any differences between the examined specimens of *F. nadari* and *F. sphinx*. Consequently, *F. sphinx* is regarded as junior synonym of the former species.

Type material examined *F nadari* – Lectotype, male (MNHN)[herewith designated]. "[small, pale label] \ Jaffa [handwritten, somewhat illegible] \ type [yellowish label, handwritten] \ TYPE [red label, printed] \ MUSÉUM PARIS COLL M. PIC [printed] \ F nadari Pic ou cursor Laf ? [handwritten]" Paralectotype, female (MNHN) "[small, pale label] \ Jericho [handwritten] \ type [yellowish label, handwritten] \ TYPE [red label, printed] \ MUSÉUM PARIS COLL M PIC [printed]". *F. sphinx* – Lectotype, male (NHMW))[herewith designated]. "Cairo Aegypt [printed] \ [male mark] [printed] \ TYPE [red label, printed] \ F. sphinx Kr det. V. Krekich [species name handwritten] Paralectotypes: 2 males, 1 female (NHMW) same data as lectotype, except "[female mark]" [printed, in female]; 1 male (MNHN, coll M Pic): same data as lectotype, in addition with label "736." [printed] Additional specimens examined 1 male (CKD), E-Jordan, Wadi Schaib, 200 m, ix 1956, J. Klapperich leg , 4 males, 1 female (CKD), E-Jordan, Jerash, 14 vi 1968, J & S Klapperich leg., 1 male (CKD), Izrael, Dalia, 20 vii.1976, O Mehl leg., 1 female (NMPC), Izrael, Jerusalem, 24.ii 1942, Houška leg ; 2 males, 1 female (BMNH), Izrael, Beyrouth, Frater Jean lgt ; 1 female (CKD), Turkey, Adıyman prov , Karadut, 9-12 vii 1997, P. Kresl leg.; 1 female (NMPC), Turkey, Adana, 1-3.viii.1947, Exp N Mus. ČSR; 1 female (NMPC), Turkey, Anatolia, Abaçılar (Cakıt), 7 viii 1947, Exp N. Mus. ČSR.

Distribution. Egypt, Syria, Izrael, Jordan (Uhmann 1985, 1988), south Turkey. Records from Iran ("Persien, Luristan") by Uhmann (1985) are based on misidentified specimens of *F. phymopes* Bonadona, 1964.

Formicomus suratus **Baudi, 1879**

Formicomus suratus Baudi, 1879 87.

Type material examined Holotype, male (IRSN)[mounted on small, triangular label]: "Coll R I. Sc N B Maroc: Tanger Coll J Thomson [partly printed, "Tanger" handwitten] \ det Baudi 1879 \ F. suratus Baudi n. sp [male *mark] [older, handwritten label, mounted on the preceding label]* \ TYPE *[red label with black frame, printed]* \ Formicomus suratus Baudi ~~dét~~ rev J. B. v Krekich 1913 [Krekich's name printed]"

Remarks. Baudi (1879) described *F. suratus* from single specimen from Maroc ("Tanger") and mentioned its similarity with *F. braminus* LaFerté-Sénectère, 1849. The examination of the holotype specimen confirmed, that *F. suratus* belongs to the *Formicomus braminus* species-group, established by Krekich-Strassoldo (1929). This group is distributed exclusively in the Oriental and the East-Palaearctic region, reaching its westernmost limits in eastern Afghanistan (*F. nuristanicus* Bonadona, 1964). Considering distribution of the *F. braminus* species-group, the single known record of *F. suratus* and similarity of this species with *F. barbipes* Krekich-Strassoldo, 1931 from India, the type specimen of *F. suratus* is regarded as either introduced to Morocco or mislabelled.

Formicomus bukharensis sp. n.

(Figs 3–9)

Description (male). Head dark brown; pronotum pale rufous-brown, vaulted antero-lateral sides sometimes darkened, elytra largely dark brown to brown-black, basal fourth yellowish-brown with rufous tinge (as in several specimens, the extreme base of elytra, scutellum and suture can be darkened and thus the paler colouration is reduced to paired, latero-basal, vaguely outlined spots extendig from elytral humeri posteriorly); legs rufous brown, with distal, clavate portion of femora darkened; mouth-parts and palpi rufous-brown; antennae rufous brown, darkened in distal half.

Head round shaped, including eyes 1.12 times as long as wide, somewhat widely rounded posteriorly (posterior arch nearly semicircular); hind temporal angles rounded. Eyes comparatively small, moderately convex, moderately protruding from lateral outlines of head. Neck short, distinctly differentiated from head. Dorsal surface of head finely, somewhat sparsely (especially posterodorsally), but distinctly punctured, with pale decumbent and few erect setae.

Pronotum 1.3 times as long as wide, narrower than head including eyes, regularly rounded anteriorly, distinctly impressed (constricted in dorsal view) laterally and slightly convex to flattened dorsally in posterior half. Dorsal surface of pronotum finely, but distinctly punctured, similarly as head, punctures somewhat more densely spaced medially in anterior half, becoming gradually sparser towards lateral sides and base; basal, narrowed portion of pronotum on each side (dorsolaterally) with short strip of rather densely spaced, nearly contiguous punctures, bearing medially directed setae, its dorsal face more sparsely punctured medially and smooth and glossy before base; lateral sides with only few scattered punctures anteriorly, smooth and glossy ventro-laterally and before latero-basal ipressions. Pubescence similar to that of head. Basal margin of pronotum distinctly bordered.

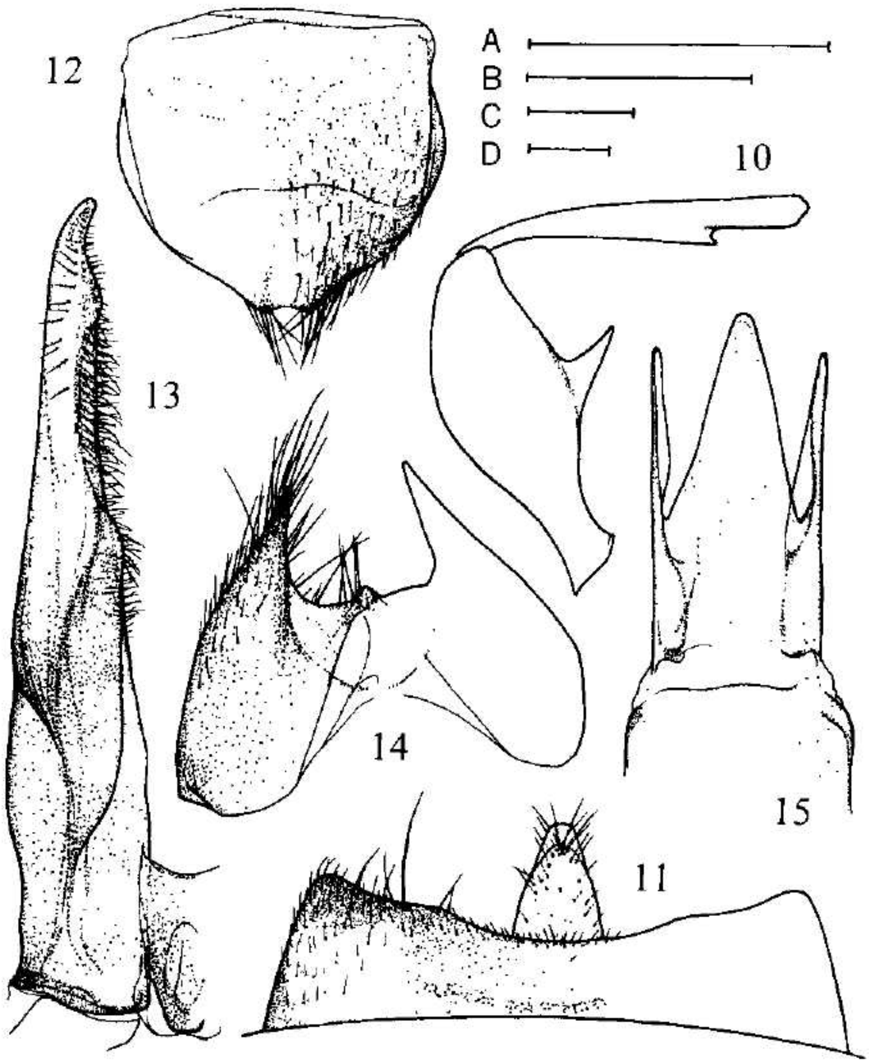
Mesosternum simple; metasternum moderately impressed postero-medially.

Elytra 1.65 times as long as wide; elytral humeri distinct; postscutellar impression slight; hind membranous wings well developed. Surface of elytra sparsely punctured. Pubescence distinctly double, composed of shorter decumbent setae and numerous much longer, semierect setae.

Antennae moderately exceeding elytral humeri; segment I 1.8 times as long as wide; segment X 1.4 times as long as wide; segment XI 2.7 times as long as wide and 1.7 times as long as segment X.

All femora distinctly clavate; the penultimate segment of metatarsi moderately dilated apically, with terminal segment implanted subapically dorsally (resembling more likely the condition in Fig. 29); character of connection of the last two tarsal segments in mesotarsi appears intermediate between those in Figs 29, 30. Front legs modified (Fig. 3); profemora with long, bluntly pointed process; protibia with distinctly protruding edge, rather abruptly shortened distally.

Sternite VII (Fig. 4) with posterior margin deeply emarginate, with short, wide medial process, bearing about fifteen, long setae arranged along its apical margin. Tergite VII (Fig. 5) with posterior



Figs 10–15. *Formiconus parallelus* Marseul (male): 10 – front leg; 11 – sternite VII; 12 – tergite VII; 13 – prong of sternite VIII, dorsal aspect; 14 – tergite VIII; 15 – apical portion of tegmen of aedeagus. Scale (0.5 mm): A – 14; B – 10, 12. (0.1 mm): C – 13, 15, D – 11.

margin simply rounded. Sternite VIII (Figs 6, 7) of somewhat complicated structure, with a pair of medial prongs and two flattened lobes on each side laterally; prongs dilated dorsally close behind mid-length into small lobe, narrowed towards pointed apex; medial surface of prongs, except finer scattered setae, with a cluster of stiff setae dorso-medially; dorso-lateral lobes of sternite VIII narrow, curved, pointed apically; ventro-lateral lobes rather wide, rounded apically, long and densely setose along margins and on outer surface. Tergite VIII (Fig. 8) composed of a pair of sclerotized plates, narrowly connected medially, rounded apically. Aedeagus with apical portion of tegmen distinctly shorter, 0.3 times as long as the basal portion; apex of tegmen (Fig. 9) trilobed.

SEXUAL DIMORPHISM. Female externally identical with male, but differs by the simple front legs and by the simply shaped abdominal segments VII, VIII.

LENGTH. 3.7–3.9 mm.

TYPE MATERIAL. Holotype, male (NMPC). "USSR – Uzbekistan Bukhara district 22 - 25 May 1990 \ 30 km SE of Kagan near Amu-Bukhara canal semidesert territory Zd Jindra lgt" Paratypes 3 males, 1 female (CKD) "S-KAZAKHSTAN, Koktal garden, 15 vi 1992 K. Deneš leg", 1 male (KMVC). "UZBEKISTAN BUKHARA distr M. Mikát leg \ 20–30 km SE Kagan Karaulbazar 30 V 1987", 1 female (NHMW). "Stat. Dshussaly Syrdarja Geb \ Breit \ Nemrod Laf. det. v. Krekich".

DISTRIBUTION. So far known from Uzbekistan and south Kazakhstan.

ETYMOLOGY. Named after Bukhara city, an ancient metropolis of Central Asia.

DIFFERENTIAL DIAGNOSIS. *F. bukharensis* sp. n. is no doubt very closely related to *F. latro* LaFerté-Sénectère, 1849, *F. hauseri* Pic, 1897 and *F. volkonskyi* Pic, 1942. While these already known species show only minor differences in some of the male characters (figured by Bucciarelli, 1980 for *F. latro*) *F. bukharensis* sp. n. can be easily distinguished within this group by the form of sternite VIII. Apart from secondary sexual characters, it differs from sympatric *F. hauseri* by pronotum distinctly paler coloured than head and bicoloured elytra (body in *F. hauseri* unicoloured piceous-black), by the finer punctation of head and pronotum and by the double pubescence of elytra, comprising numerous long, semierect setae (elytral pubescence in *F. hauseri* rather uniformly short, with only few erect setae, not longer than the decumbent ones).

Based on the original description, *F. biskrensis* Fairmaire, 1883 from Algeria is apparently related to *F. bukharensis* sp. n., however this species is in my opinion close to or even identical with *F. latro*.

Formicomus parallelus Marseul, 1879

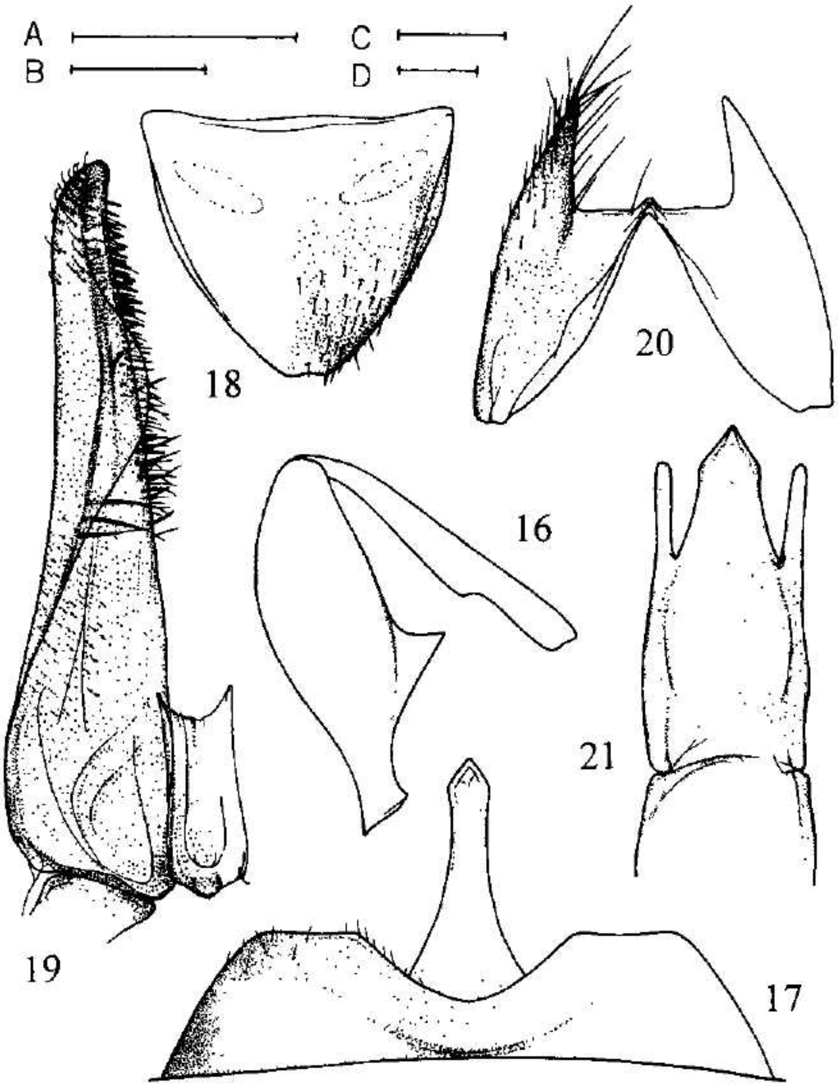
(Figs 10–15)

Formicomus parallelus Marseul, 1879: 48, 50.
Formicomus nemrod Marseul, 1879: 47.

REDESCRIPTION (male). Rufous-brown; legs and distal half of antennae darkened; elytra largely brown-black to black, with the basal fourth rufous-brown.

Head round shaped, including eyes 1.2 times as long as wide, regularly rounded posteriorly (posterior arch semicircular); temporal angles entirely obsolete. Eyes comparatively large, moderately convex. Neck short, clearly differentiated from head. Dorsal surface of head very finely, somewhat sparsely punctured; pale pubescence composed of shorter, decumbent to semierect and few erect setae.

Pronotum 1.4 times as long as wide, narrower than head, regularly rounded anteriorly, distinctly impressed (constricted in dorsal view) laterally and slightly convex to flattened dorsally in posterior half. Dorsal surface of pronotum punctured and pubescent similarly as head, slightly denser mid-dorsally; lateral sides with only few scattered punctures anteriorly, otherwise rather smooth and



Figs 16–21. *Formicomus jelineki* sp. n. (male): 16 – front leg; 17 – sternite VII; 18 – tergite VII; 19 – prong of sternite VIII, dorsal aspect; 20 – tergite VIII; 21 – apical portion of tegmen of aedeagus. Scale (0.5 mm): A – 16, 18. (0.1 mm): B – 19; C – 21; D – 17, 20.

glossy especially before latero-basal impressions; bottom of latero-basal impressions finely wrinkled; base on each side (dorso-laterally) with short longitudinal strip of more densely spaced, coarser punctures, bearing medially directed setae. Basal margin of pronotum distinctly bordered.

Mesosternum simply shaped. Metasternum moderately impressed postero-medially, close before posterior margin.

Elytra longitudinally oval, 1.9 times as long as wide, rounded apically; humeri distinctly angulate; hind membranous wings well developed; postscutellar impression slightly indicated. Elytral punctation distinctly double, composed of coarser, more widely spaced, setigerous punctures, bearing shorter to comparatively long, decumbent to semierect, pale setae, and much finer, more densely spaced punctures.

Antennae comparatively short, at most reaching elytral humeri, moderately enlarged distally; segment I twice as long as wide; segment X 1.5 times as long as wide; segment XI 2.5 times as long as wide, 1.5 times as long as segment X.

All femora distinctly clavate; all tarsi shorter than tibia; the penultimate segment of all tarsi flattened distally, with the terminal segment implanted at its mid-length, dorsally, similarly as in Fig. 30. Front legs modified (Fig. 10); profemora with long, thorn-like, pointed process; protibia with a distinct, simple protrusion in distal half.

Sternite VII (Fig. 11) with posterior margin shallowly, rather widely emarginate, with wide medial process, rounded apically, setose on its dorsal side, subapically. Tergite VII (Fig. 12) narrowed and moderately produced apically; apical margin slightly emarginate medially. Sternite VIII (Fig. 13) with a pair of long, straight prongs, moderately dilated dorsally at about mid-length into longitudinal, flattened lobe; apices of prongs bluntly rounded, slightly curved mediad; medial margin densely setose in distal half. Tergite VIII (Fig. 14) composed of a pair of plates, narrowly connected medially, strongly narrowed, pointed and long setose apically. Aedeagus with apical portion of tegmen distinctly shorter, 0.4 times as long as the basal portion; apex of tegmen (Fig. 15) trilobed, middle lobe dorso-ventrally flattened, wider and moderately longer than lateral lobes, narrowing towards bluntly pointed apex, lateral lobes flattened laterally.

SEXUAL DIMORPHISM. Female externally identical with male, but differs by the simple front legs and by the simply shaped abdominal segments VII,VIII.

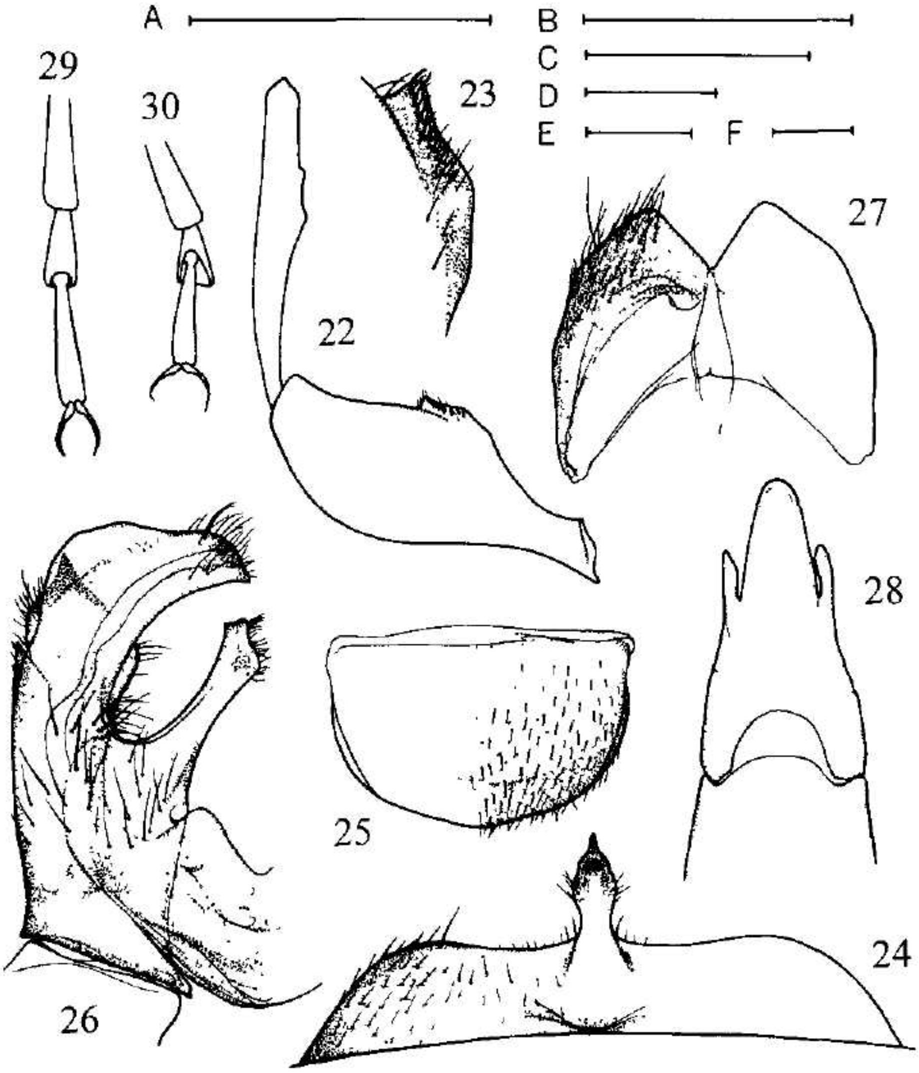
LENGTH. 3.9–5.1 mm.

TYPE MATERIAL Lectotype, male (MNHN)[herewith designated, prep label with pink strip at base, bearing handwritten sex-markings} "Formicomus parallelus pedestris Mesopot Shp 78 [round yellow label, handwritten, "Shp" illegible] \ 3 Nemrod – Laf 75 M 50 Mésop brevipilis Desb Op 42. [printed label, pinned separately on bottom] Paralectotypes. 1 female (MNHN), mounted on the same label as Lectotype, 1 male, 1 female (MNHN)[mounted on the same label] "Formicomus pedestris Mesopot Shp 78" [round yellow label, handwritten], the second label common with Lectotype, pinned on bottom.

ADDITIONAL SPECIMENS EXAMINED 1 male (MNHN, coll Marseul)· "Formicomus nemrod Laf. Bagdad 67 [round pale label, handwritten] \ 4 parallelus – Mars 50 Mésop. [printed label, pinned separately on bottom]"; 1 female (MNHN, coll Pic) "Bagdad \ Nemrod Laf (ex coll Mars)", 18 males, 7 females (NMPC), Iraq, Baghdad, Kálalová legit , 1 female (CKD), Iraq, Abu-Ghraib, iv.1984, Ing. Smatana leg., 1 male, 1 female (BMNH, NHMW), "Mesopot \ F Bates 81 19", 5 males, 1 female (NHMW), Iraq, Mosul; 1 female (NHMW), Iraq, Baghdad, 1 male (NHMW)· "Mesopot Exp. Nat. G V 1910"; 1 female (BMNH), "Mesopot \ Sharp Coll 1905 313", 1male, 1 female (BMNH), Iraq, Baghdad, vi-viii.1928, N. Scott lgt.

DISTRIBUTION. So far known only from Iraq. Records from Saudi Arabia by Uhmann (1998) are based on misidentified material, comprising several different species, which I am so far not able to identify reliably.

REMARKS. Marseul did not use "type" labels or any special marking useful for distinguishing of the type specimens. Generally, the specimens are supplied by the two different kinds of labels, round pinned label and narrow angular label, placed separately on bottom of box. In the case of *F.*



Figs 22–30 22–28 *Formicomus persicus* sp. n (male) 22 – front leg; 23 – detail of profemoral process; 24 – sternite VII; 25 – tergite VII; 26 – prong of sternite VIII, dorsal aspect, 27 – tergite VIII; 28 – apical portion of tegmen of aedeagus. 29, 30 the last two segments of metatarsus: 29 – *F pedestris* (Rossi); 30 – *F nadari* Pic. Scale (0 5 mm): A – 27; B – 22, C – 25 (0 1 mm). D – 2 , 26, E – 28–30, F – 24

parallelus, these two labels bear rather contradictory data (different species names), however, the following two facts led to the decision about priority of round labels and designation of the type specimens 1) the two syntypes of *F parallelus* bear data "Formicomus parallelus pedestris Mesopot " Marseul (1879) mentioned similarity of *F parallelus* and *F pedestris* (Rossi, 1790), but he did not record the latter species from "Mesopotamia", 2) in the key to species of *Formicomus* by Marseul (1879), *F parallelus* and *F nemrod* LaFerté-Sénectère, 1849 form a couplet, differing from other species by the larger size and the elongate, parallel elytra As to mutual differences, *F nemrod* is unicoloured rufous, while *F parallelus* is dark brown, with pale transverse band at base of dark elytra The syntypes of *F parallelus* and the single specimen of *F nemrod* of Marseul's collection (= the first male specimen listed in the additionally examined material) show the same differences in colouration Since these five specimens and another specimen in Pic's collection, with data "nemrod Laf ex coll Mars ", belong in fact to the same species, it is believed, that Marseul later considered *F parallelus* identical with *F nemrod* and interchanged position of the respective specimens in his collection (having studied both syntypes of *F nemrod*, I do not agree with Marseul's opinion and consider *F parallelus* clearly different from *F nemrod*)

Dealing with chilean Anthicidae, Solier (1851) named one of his new species *Formicomus parallelus* Later, Pic (1911) and Blackwelder (1954) listed this species in the genus *Anthicus* (in wide sense) I have seen the two syntypes of *Formicomus parallelus* Solier in MNHN, bearing the following data "15 43 [roud green label] \ Formicomus parallelus Sol Sa Rosa Coquicubo [handwritten, partly illegible] \ MUSEUM PARIS CHILI Gay 15-43 [printed]" They quite surely belong to different genus (very probably *Ischyropalpus* LaFerté-Sénectère, 1849) According to ICZN § 57 (h) (i), a replacement name for *F parallelus* Marseul is not necessary

***Formicomus jelineki* sp. n.**

(Figs 16–21)

DESCRIPTION (male) Rufous-brown, the last three antennal segments darkened, elytra largely brown-black to black, with the basal fourth rufous-brown

Head round shaped, including eyes 1 2 times as long as wide, regularly rounded posteriorly (posterior arch semicircular), temporal angles entirely obsolete Eyes large, moderately convex, moderately protruding from lateral outlines of head Neck short, distinctly differentiated from head Dorsal surface of head distinctly, somewhat sparsely punctured, very finely corrugated anteriorly and along medial margins of eyes, pale pubescence composed of short, decumbent and few erect setae

Pronotum 1 3 times as long as wide, distinctly narrower than head, regularly rounded anteriorly, distinctly impressed (constricted in dorsal view) laterally and slightly convex to flattened (not impressed) dorsally in posterior half Dorsal surface of pronotum, in comparison with head, somewhat more densely punctured, lateral sides with only few, scattered punctures anteriorly, smooth and glossy, especially before latero-basal impressions, bottom of latero-basal impressions short finely wrinkled, basal, narrowed portion of pronotum finely longitudinally wrinkled and more densely punctured dorso-laterally and with several, fine transverse wrinkles dorsally Basal margin of pronotum distinctly bordered

Mesosternum simply shaped Metasternum moderately impressed postero-medially, close before posterior margin

Elytra longitudinally oval, 1 9 times as long as wide, rounded apically, humeri distinctly angulate, hind membranous wings well developed, postscutellar impression slightly indicated Elytral punctation double, composed of coarser, more widely spaced, setigerous punctures, bearing shorter, mostly decumbent, pale setae, and much finer, more densely spaced punctures

Antennae long and slender, distinctly exceeding elytral humeri, segment I twice as long as wide, segment X 1 9 times as long as wide, segment XI 2 9 times as long as wide, 1 3 times as long as segment X

All femora distinctly clavate, all tarsi shorter than tibia, the penultimate segment of all tarsi somewhat flattened distally, with the terminal segment implanted at its mid-length, dorsally, similarly as in Fig 30 Front legs modified (Fig 16), profemora with rather strong, somewhat proximally situated, pointed process, protibia abruptly, moderately narrowed in distal half

Sternite VII (Fig 17) with posterior margin distinctly emarginate, with conspicuously long, flattened medial process, narrowing towards somewhat triangulate, bluntly pointed apex Tergite VII (Fig 18) with posterior margin very slightly emarginate apically Sternite VIII (Fig 19) with a pair of straight, simple prongs, moderately dilated dorso-medially into longitudinal flattened lobe, apex of prongs bluntly rounded, medial margin of prongs short, densely setose Tergite VIII (Fig 20) composed of two, paired plates, narrowly connected medially, strongly narrowed and pointed apically Aedeagus with apical portion of tegmen distinctly shorter, 0 3 times as long as the basal portion, apex of tegmen (Fig 21) trilobed, middle lobe distinctly wider and moderately longer than lateral lobes

Sexual dimorphism Female in general agrees with male, but differs by the following characters antennae shorter, segments IV–XI distinctly less elongate, segment X 1 5 times as long as wide, segment XI 2 5 times as long as wide, front legs and abdominal segments VII, VIII simply shaped

Length 3 5–4 5 mm

Type material Holotype male (NMPC) "S Iran, 30 km E Kazerun, 1300 m, 8–10 6 1973 \ Loc No 229 Exp Nat Mus Praha \ Formicomus nobilis Falderm det G Uhmann 1992" Paratypes 4 males, 8 females (NMPC), 2 males 3 females (CUP) same data as holotype, two of them lacking the last, determination label, 1 male (NMPC) SW Iran Dasht e Arzhan (Shur) 5 7 1970 \ Loc No 44 Exp Nat Mus Praha",1 male 2 females (NMPC) SW Iran Kazerun 5 6 7 1970 \ Loc No 45 Exp Nat Mus Praha"

Distribution Iran

Etymology Dedicated to Dr Josef Jelínek (NMPC)

Differential diagnosis *Formicomus jelineki* sp n is closely related to the preceding species, *F parallelus* It differs from the latter by the following characters eyes slightly larger, more convex and protruding, antennae longer and less extensively darkened distally, dorsal surface of head and pronotum somewhat more coarsely puncured, base of pronotum finely wrinkled dorsally, pubescence of elytra more decumbent and uniform in length, lacking distinctly longer setae, male profemoral process stronger, situated more proximally, medial process of male sternite VIII distinctly longer, asetose, prongs of male sternite VIII shorter, more simply shaped

***Formicomus persicus* sp. n.**

(Figs 22–28)

Description (male) Dark rufous-brown, elytra darker, largely brown to brown-black, with the basal fourth more or less distinctly paler, rufous-brown

Head 1 2 times as long as wide, regularly rounded posteriorly (posterior arch semicircular) Eyes comparatively small, moderately convex, moderately protruding from lateral outlines of head Neck short, clearly differentiated from head Dorsal surface of head finely, but distinctly punctured, with short, decumbent and few erect setae

Pronotum 1 36 times as long as wide, regularly rounded anteriorly, moderately impressed (constricted in dorsal view) laterally and slightly convex (not impressed) dorsally in posterior half Punctation and pubescence of pronotum similar to that of head, slightly denser mid-dorsally and becoming gradually sparser towards lateral sides in anterior half; basal, narrowed portion of pronotum more or less distinctly longitudinally wrinkled on each side, dorso-laterally; lateral sides more finely and less densely punctured, especially before latero-basal impressions; bottom of latero-basal impressions with only few, short, inconspicuous wrinkles ventro-laterally; base of pronotum distinctly bordered.

Elytra oval, 1.67 times as long as wide, widely rounded to subtruncate apically in dorso-caudal view; humeri and postscutellar impression entirely obsolete; hind, membranous wings reduced. Elytral punctures more widely spaced than those on head, bearing longer decumbent to semierect pale setae; interspaces among setigerous punctures very sparsely and much more finely punctured.

Both mesosternum and metasternum simply shaped.

Antennae rather strong, exceeding base of elytra; segment I short, 1.7 times as long as wide; segment X 1.37 times as long as wide; segment XI 2.4 times as long as wide, 1.7 times as long as segment X.

All femora distincly clavate; all tarsi shorter than tibia; the penultimate segment of all tarsi (especially meso and metatarsi) narrow, somewhat obliquely truncate apically, with the terminal segment implanted apically, similarly as in Fig. 29. Front legs modified (Fig. 22); profemora with short, wide, rather strong process, armed with about ten, thick, blunt setae (Fig. 23), arranged along its apical edge, and a number of finer, pointed setae; protibia moderately enlarged and with two minute protuberances in distal half.

Sternite VII (Fig. 24) with strong medial process, enlarged at its mid-length, narrowed and pointed apically; dorsal surface of process short setose. Tergite VII (Fig. 25) with posterior margin simply rounded. Sternite VIII (Fig. 26) with a pair of strong, dorso-ventrally flattened, arcuately converging prongs; each prong medio-basally with a long process, somewhat enlarged and short setose apically; mid-dorsal surface of prongs with number of long, sparsely scattered setae. Tergite VIII (Fig. 27) composed of a pair of plates, narrowly connected medially, angulately rounded apically. Tegmen of aedeagus (Fig. 28) trilobed apically; middle lobe much wider and longer than lateral lobes.

SEXUAL DIMORPHISM. Female externally identical with male, but differs by the simple front legs and by the simply shaped abdominal segments VII,VIII.

LENGTH. 2.9–3.7 mm.

TYPE MATERIAL. Holotype, male (NMPC): "E. Iran, 1100 m, 33 km W Sabzvaran 6–7.5. 1973 \ Loc. No 189 Exp. Nat. Mus. Praha". Paratypes: 4 males, 5 females (NMPC), same data as holotype.

DISTRIBUTION. Iran.

ETYMOLOGY. Named after the ancient empire Persia, extending in the past on the territory of present Iran.

DIFFERENTIAL DIAGNOSIS. *Formicomus persicus* sp. n. can be distinguished from all the Palaearctic species by the obsolete elytral humeri in combination with the form of profemoral process and the abdominal sternites VII, VIII in male.

Acknowledgements

I am very gratefull to all curators who loaned me specimens in their care, namely N. Berti (MNHN); M. Brendell (BMNH); M. Cludts and K. Desender (IRSN); J. Jelinek (NMPC); M. Mikát (KMVC); H. Schönmann (NHMW); G. Uhmann (Pressath). Furthermore, my sincere thanks are due to S. Bečvář (Institute of Entomology, České Budějovice) for the SEM photographs, and to D. Král (Charles University, Prague) for reviewing the manuscript.

REFERENCES

Baudi F S 1876 Formicomus suratus n sp *Bull Ann Soc Entomol Belg* **22** 87–88

Blackwelder R E 1945 Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America Part 3 *Bull U S Natl Mus* **185** 343–550

Hille J C van 1977 Species of the genus *Formicomus* Laf from North-East Africa and adjacent parts of the Arabian Peninsula (Coleoptera Anthicidae) *Entomol Scand* **8** 197–204

Chandler D S 1999 Publication Dates of Papers on the Anthicidae (Coleoptera) by the Marquis F T de Laferte-Senectere *Trans Am Entomol Soc* **125** 433–439

Krekich-Strassoldo H von 1919 Beitrage zur Kenntnis der Anthiciden und Hylophiliden (Col) *Entomol Mitt* **8** 166–175

Krekich-Strassoldo H von 1929 Die Anthiciden der Philippinen II *Philip J Sci* **40** 453–481

LaFerté-Sénectère M F de 1849a Formicomus (Lavraison 7, No 25) Pp 1–25 In Guerin-Meneville F -E (ed) *Species et iconographie generique des Animaux Articules ou representation des genres, avec leur description et celle de toutes les especes de cette grande division du regne animal Premiere Partie Insectes Coleopteres* Paris Fain et Thunot, 78 pp

LaFerté-Sénectère M F de 1849b *Monographie des Anthicus et genres voisins Coleopteres Heteromeres de la tribu des Trachelides* Paris Sapia, 340 pp

Marseul S de 1879 Monographie des Anthicide de l'Ancien-Monde *L Abeille* **17** 1–268

Pic M 1893 Anthicides nouveaux de l'Ancien monde *Feuille Jeun Nat* **23** 175–176

Pic M 1907 Anthicides recueillis en Erythree par le Dr Ch Figini *Ann Mus Civ Stor Natur Genova* **43** 63–65

Pic M 1894 Examen des Anthicides de la collection H Tourmer *LEchange* **10** 64–65

Pic M 1911 Anthicidae In Junk W & Schenkling S (eds) *Coleopterorum Catalogus* 36 Berlin V Junk 102 pp

Pic M 1939 Mission scientifique de l'Omo Coleoptera XVIII Rhizopaussidae, Pedilidae, Hylophilidae, Anthicidae, Scraptiidae, Mordellidae, Oedemeridae, Alleculidae *Mem Mus Histor Natur Paris* **1939** 153–170

Solier A J J 1851 Fauna Chilena Insectos Orden III Coleopteros XXXVII Anthicoides In Gay C 1851 *Histor Fis Polit Chile, Zool* **5** 275–278

Uhmann G 1985 Palaarktische Anthiciden (Coleoptera) der Ungarischen Naturwissenschaftlichen Museum Budapest *Fol Entomol Hung* **46** 177–203

Uhmann G 1988 Die Anthicidae der Sammlung Johann Klapperich *Bonn Zool Beitr* **39** 395–407

Uhmann G 1998 Anthicidae (Insecta Coleoptera) from Saudi Arabia with the description of a new species *Fauna of Arabia* **17** 93–105

Acta Soc. Zool. Bohem. 64: 419–424, 2000
ISSN 1211-376X

A new wood-hoopoe (Aves: Phoeniculidae) from the early Miocene of Germany and France

Jiří MLÍKOVSKÝ[1)] & Ursula B. GÖHLICH[2)]

[1)] Institute of Geology and Paleontology, Charles University, Albertov 6, CZ–128 43 Praha 2, Czech Republic,
e-mail: mlikovsky@sendme.cz
[2)] Institut für Palaontologie und historische Geologie, Richard-Wagner-Straße 10, D–80333 Munchen, Germany;
e-mail: u.goehlich@lrz.uni-muenchen.de

Received October 25, 2000, accepted December 4, 2000
Published December 29, 2000

Abstract. A new species of wood-hoopoes, *Phirriculus pinicola* gen. n., sp. n., is described from the early Miocene of Germany. Its known occurrence is limited to the early Miocene (MN 2a-4) of France and Germany. No other record of the Phoeniculidae is known from the Neogene of Europe.

Taxonomy, Aves, Phoeniculidae, Miocene, Europe

INTRODUCTION

Wood-hoopoes are small to middle-sized arboreal birds, currently confined to the Afrotropics (Fry et al. 1988). Their fossil record is confined to unnamed forms from the early Miocene of France and Germany (Ballmann 1969b). Below we will redescribe this material, add new records from Germany, and review the fossil record of the family Phoeniculidae.

The material from Wintershof-West is deposited in the Bayerische Staatssammlung für Paläontologie und Historische Geologie (BSP) in München, Germany, the material from Saint-Gérand-le-Puy is deposited in the Muséum National d'Histoire Naturelle (MNHN) in Paris, France, and that from Petersbuch is in the private collection of M. Rummel (Coll. R.) in Weissenburg, Germany. Stratigraphical divisioning of the Neogene follows Steininger (1999).

SYSTEMATIC PALEONTOLOGY

Order Coraciiformes Forbes, 1884

Family Phoeniculidae Bonaparte, 1831

Genus *Phirriculus* gen. n.

TYPE. *Phirriculus pinicola* sp. n. (by present designation).
SPECIES INCLUDED. Type species only.
DISTRIBUTION. Early Miocene (MN 2a-4) of France and Germany.
DIFFERENTIAL DIAGNOSIS. Member of the Phoeniculidae. Differs from *Phoeniculus* in having: (1) entepicondyle on humerus less flaring laterally, (2) internal condyle on humerus more rounded, (3) border between olecranon and external cotyla on ulna straight (concave in *Phoeniculus*), (4) olecranon on ulna straight, laying in the axis of the shaft (bent palmary in *Phoeniculus*), (5) metacarpal I shorter, (6) external carpal trochlea less projecting proximally, (7) trochlea for digit III on tarsometatarsus less excavated, and (8) trochlea for digit II less flaring medially.

Table 1. Measurements of *Phirriculus pinicola* gen. n., sp. n. from the early Miocene of Europe. All measurements are in mm. Abbreviations of the localities are as follows: P = Petersbuch 38, SG = Saint-Gérand-le-Puy, WW = Wintershof-West. GL = greatest length, PW = proximal width, DW = distal width.

Bone	Locality	Number	GL	PW	DW
Humerus	SG	MNHN Av 2859	21.6	6.7	5.0
	SG	MNHN Av 2860	–	–	4.9
	SG	MNHN Av 2861	19.5*	6.4*	5.0
	SG	MNHN, uncategored	21.2	7.3	4.9
	WW	BSP 1937 II 18187	–	–	5.2
	WW	BSP 1937 II 18188	–	–	5.2
Ulna	WW	BSP 1937 II 18184	–	4.2	–
	P	Coll. R. P38-A-0001	–	4.3	–
Carpometacarpus	WW	BSP 1937 II 18179	–	4.2	–
	WW	BSP 1937 II 18180	–	4.2	–
	WW	BSP 1937 II 18181	–	4.3	–
	WW	BSP 1937 II 18182	–	4.2	–
	WW	BSP 1937 II 18183	–	4.4	–
Tarsometatarsus	WW	BSP 1937 II 18186	–	–	ca. 2.9

* Data after Ballmann (1969b), the specimen has been almost destroyed during cast making, and only its distal end is now measurable. *Note that the values are incorrectly printed in* Ballmann *(1969b: 47), where the decimal* separator is misplaced.

** Data after Milne-Edwards (1869–1871), proximal end is now too damaged to be measurable.

Etymology. Arbitrary combination of *Phoeniculus* Jarocki, 1821 and *Irrisor* Lesson, 1831, two synonymous names applied to the modern wood-hoopoes.

Phirriculus pinicola sp. n.

(Figs. 1–8)

Holotype. Distal end of left humerus (BSP 1937-II-18188) from the early Miocene (MN 3a) of Wintershof-West, Bavaria, Germany.

Referred material. Wintershof-West: distal end of left humerus (BSP 1937-II-18187), proximal end of right ulna (BSP 1937-II-18184), 4 proximal ends of left carpometacarpi (BSP 1937-II-18179 through 18182), proximal end of right carpometacarpus (BSP 1937-II-18183), and distal end of left tarsometatarsus (BSP 1937-II-18186); Petersbuch 38, proximal end of right ulna (coll. Rummel, P38-A-0001); Saint-Gérand-le-Puy: 3 left humeri (MNHN Av-2860, Av-2861, and an uncatalogued specimen), distal end of left humerus (MNHN Av-2859).

Diagnosis. Same as for the genus.

Measurements. See Table 1.

Etymology. The "pine-runner", from *Pinus*, modern genus of coniferous trees and *cola*, latinized from Greek *kola*, meaning a runner. The name indicates, that the bird was possibly creeping – in the manner of modern tree-hoopoes – on the trunks of *Pinus* conifers, which were abundant in Europe in the early Miocene (see e.g. Bůžek et al. 1996). The name is a substantive in apposition.

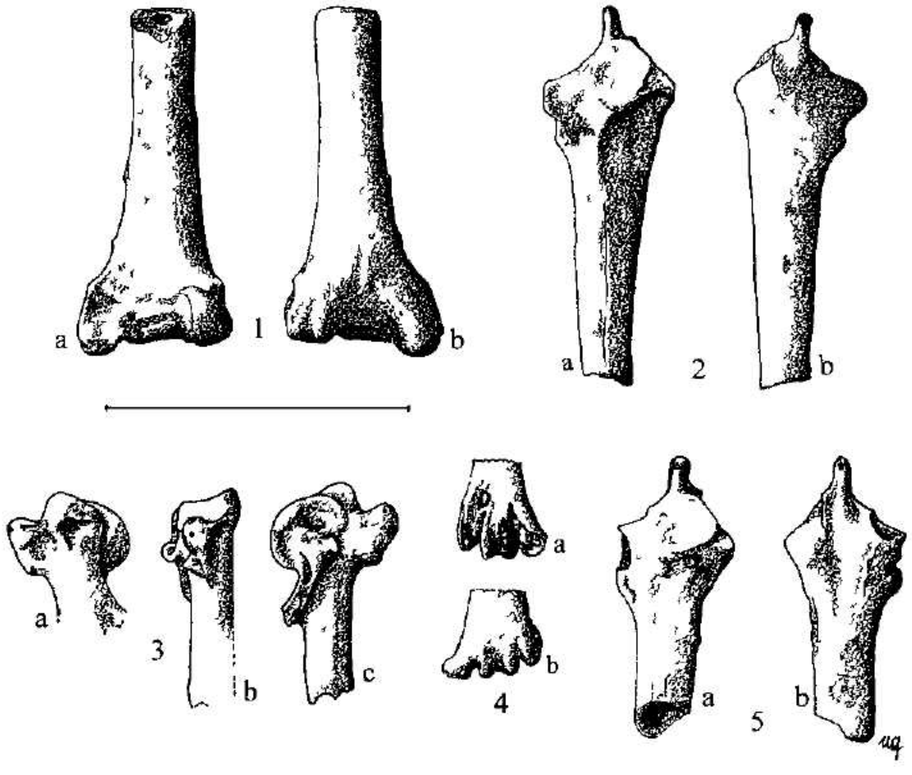
Distribution. Early Miocene (MN 2a) of Saint-Gérand-le-Puy, Dept. Allier, France; early Miocene (MN 3) of Wintershof-West, Eichstätt Co., Bavaria, Germany; and early Miocene (MN 4) of Petersbuch 38, Eichstätt Co., Bavaria, Germany.

Remarks on the material from Wintershof-West: Ballmann (1969b) listed among the bones he attributed to an unnamed wood-hoopoe from Wintershof-West distal end of tibiotarsus (BSP 1937-II-

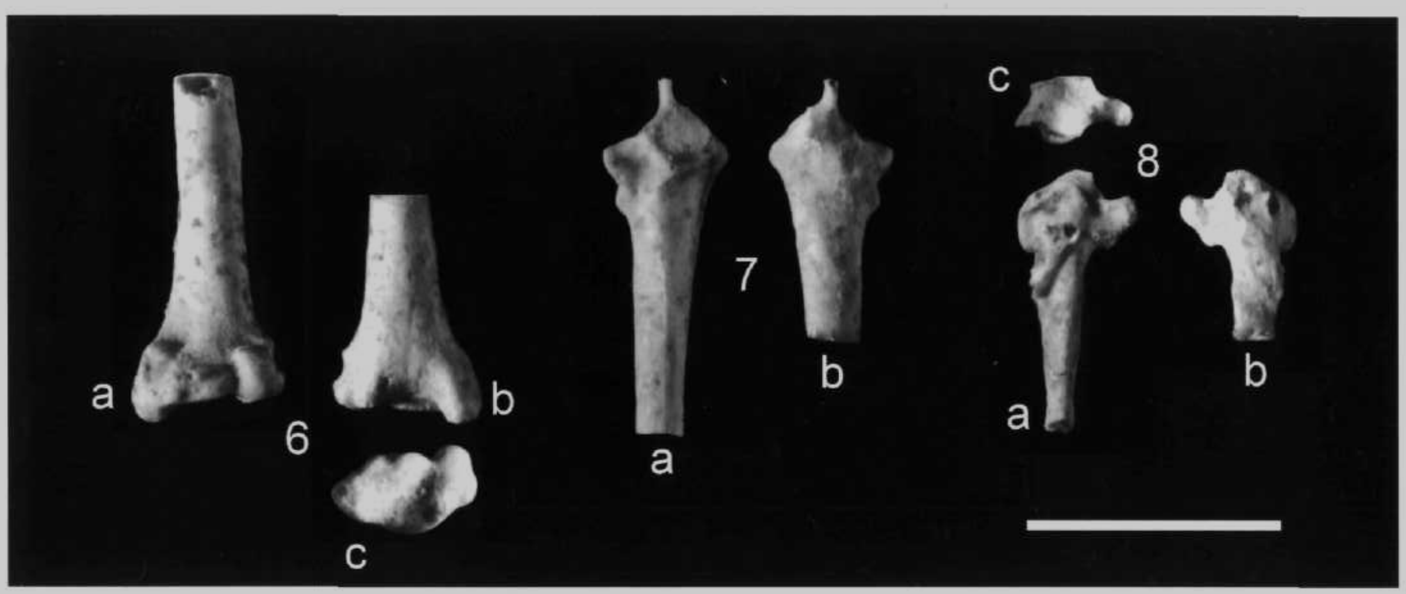
18185) This specimen differs from the tibiotarsi of the Phoeniculidae, and agrees with those of the Passeriformes in being latero-medially narrow and antero-posteriorly deep, and in having trochleae diverging (not parallel) and distal end of narrow in comparison to the trochleae This tibiotarsus belongs thus to a small indeterminate songbird, not to a wood-hoopoe

Ballmann (1969b) believed that phoeniculid bones from Wintershof-West belong to a larger wood-hoopoe than those from Saint-Gerand-le-Puy Our comparisons do not support this view (see Tab 1) *Phirriculus pinicola* gen n , sp n belonged to small wood-hoopoes, approaching in size the modern Abyssinian Scimitar-billed Wood-Hoopoe *Phoeniculus minor* (Ruppel, 1845) and the Lesser Wood-Hoopoe *Phoeniculus aterrimus* (Stephens, 1826)

Remarks on the material from Saint-Gerand-le-Puy Milne-Edwards (1871 392–393) based his *Limnatornis paludicola* on a right humerus from the early Miocene (MN 2a) of Saint-Gérand-le-Puy in France, mentioning in this respect also another two humeri from the same site Brodkorb (1971 244) erroneously considered all the three humeri syntypes of *Limnatornis paludicola* One



Figs 1–5 *Phirriculus pinicola* gen n sp n 1 – distal end of humerus (BSP 1937 II 18188, holotype), a cranial view b caudal view, 2 – proximal end of ulna (BSP 1937 II 18184) a cranial view b caudal view 3 proximal end of carpometacarpus (BSP 1937 II 18179), a dorsal view, b cranial view c ventral view 4 – distal end of tarsometatarsus (BSP 1937 II 18186) a plantar view b dorsal view 5 – proximal end of ulna (Coll Rummel P38-A-0001), a cranial view b caudal view Scale bar = 10 mm



Figs. 6–8. *Phirriculus pinicola* gen. n., sp. n. 6 – distal end of humerus (BSP 1937 II 18188; holotype), a: cranial view, b: caudal view, c: distal view; 7 – proximal end of ulna (BSP 1937 II 18184), a: cranial view, b: caudal view; 8 – proximal end of carpometacarpus (BSP 1937 II 18179), a: dorsal view, b: ventral view, c: proximal view. Scale bar = 10 mm.

of us (JM) found during his study of the fossil birds at the MNHN five humeri labeled with the name *Limnatornis paludicola*, four of which are referred here to *Phirriculus pinicola* gen. n., sp. n.

(1) The specimen Av-2858 is a complete right humerus with a slightly damaged distal end. It was figured by Milne-Edwards (1869–1871, pl. 176, fig. 14–18). Milne-Edwards (1869–1871: 392) erroneously stated, that this specimen is figured on pl. 176, fig. 8–13, but the detailed description, data on the size of the specimen, and its direct comparison with the figures in Milne-Edwards (1869–1871) clearly show that this is the specimen upon which *Limnatornis paludicola* was based, and that it is figured on pl. 176, fig. 14–18 (see also Lambrecht 1933: 624). The bone belongs to the Coliidae (see also Ballmann 1969a, Rich & Haarhoff 1985), and the taxonomic status of *Limnatornis paludicola* Milne-Edwards will thus be discussed elsewhere (Mlíkovský in prep.).

(2) The specimen Av-2859 is a complete left humerus. It was described by Milne-Edwards (1869–1871: 393) as being larger than the specimen Av-2858. It was figured by Milne-Edwards (169–1871, pl. 177, fig 14–17, as correctly indicated by Milne-Edwards 1869–1871: 393). This specimen is identified here as belonging to *Phirriculus pinicola* gen. n., sp. n. The specimen is accompanied in the collections of the MNHN with an ancient etiquette "*Limnatornis paludicola major*", but this name has no standing in the zoological nomenclature.

(3) The specimen Av-2860 is a left humerus with a damaged proximal end. It was neither described, nor figured by Milne-Edwards (1869–1871), but JM found it in the same box as the specimen Av-2859. This specimen is identified here as belonging to *Phirriculus pinicola* gen. n., sp. n.

(4) The specimen Av-2861 is a left humerus, figured by Milne-Edwards (1869–1871, pl. 176, fig. 8–13, not on pl. 176, fig. 14–18 as stated by Milne-Edwards 1869–1871: 393). The figure shows that the specimen was originally in perfect state, but JM found it crushed and covered with remains of glue in June 1999. Milne-Edwards (1869–1871) mentioned this specimen as belonging to "un oiseau du meme genre" (p. 393) or to "un oiseau voisin du *Limnatornis*" (pl. 176). This specimen is identified here as belonging to *Phirriculus pinicola* n.g. n.sp.

(5) An uncatalogued specimen was found with the etiquette *Limnatornis paludicola* at MNHN in June 1999 by JM It was neither described, nor figured by Milne-Edwards (1869–1871). This specimen is identified here as belonging to *Phirriculus pinicola* gen. n., sp. n.

REMARKS. Ballmann (1969b) believed that phoeniculid bones from Wintershof-West belong to a larger wood-hoopoe than that from Saint-Gérand-le-Puy. Our comparisons do not support this view (see Tab. 1). *Limnatornis paludicola* belonged to small wood-hoopoes, approaching in size the modern Abyssinian Scimitar-billed Wood-Hoopoe *Phoeniculus minor* (Rüppel, 1845) and the Lesser Wood-Hoopoe *Phoeniculus aterrimus* (Stephens, 1826).

CONCLUDING REMARKS

The fossil record of the Phoeniculidae is limited to the early Miocene of Europe, where *Phirriculus pinicola* gen. n., sp. n. was found in France (MN 2) and Germany (MN 3–4). Today, wood-hoopoes are restricted to the Afrotropics (Fry et al. 1988). *Phirriculus pinicola* gen. n., sp. n. thus represents one of the many Afrotropical elements in the early Miocene avifaunas of Europe (see Mlíkovský 1996).

Acknowledgements

We are obliged to Michael Rummel (Weissenburg) for allowing us to study remains of fossil birds from Petersbuch 38 JM is obliged to UG for her hospitality during his visit to Munich in November 1998. JM and UG are grateful to Daniel Goujet (MNHN) for the permission to study the bones from Saint-Gérand-le-Puy at MNHN (JM in June

1999, UG in March 2000) UG was supported by the Parsyst Fellowship of the MNHN (TMR CEE ERBFMGECT 980132) and the Deutsche Forschungsgemeinschaft (DFG Fa 53/43-1)

REFERENCES

BALLMANN P 1969a Les oiseaux miocènes de La Grive-Saint-Alban (Isere) *Géobios* 2 157–204

BALLMANN P 1969b Die Vogel aus der altburdigalen Spaltenfullung von Wintershof (West) bei Eichstatt in Bayern *Zitteliana* **1** 5–60

BRODKORB P 1971 Catalogue of fossil birds Part 4 (Columbiformes through Piciformes) *Bull Florida State Mus (Biol Sci)* **15** 163–266

BUŽEK Č, HOLY F & KVAČEK J 1996 Early Miocene flora of the Cypris shale (western Bohemia) *Acta Mus Natl Pragae (B)* **52** 1–72

FRY C H, KEITH S & URBAN E K 1988 *The birds of Africa Vol 3* London Academic Press

LAMBRECHT K 1933 *Handbuch der Palaeornithologie* Berlin Gebr Borntraeger, 1024 pp

MILNE-EDWARDS A 1869–1871 *Recherches anatomiques et paléontologiques pour servir a l histoire des oiseaux fossiles de la France Vol 2* Paris G Masson, 627 pp + pls 91–200

MLIKOVSKY J 1996 Tertiary avian faunas of Europe In MLIKOVSKY J (ed) Tertiary avian localities of Europe *Acta Univ Carol (Geol)* **39** 777–818

RICH P V & HAARHOFF P J 1985 Early Pliocene Coliidae (Aves, Coliiformes) from Langebaanweg, South Africa *Ostrich* **56** 20–41

STEININGER F F 1999 Chronostratigraphy, geochronology and biochronology of the Miocene "European Land Mammal Mega-Zones (ELMMZ) and the Miocene "Mammal-Zones" Pp 9–24 In RÖSSNER G E & HEISSIG K (eds) *The Miocene Land Mammals of Europe* Munchen Verlag Dr F Pfeil

Acta Soc. Zool. Bohem. **64**: 425–435, 2000
ISSN 1211-376X

Rhopalomyia tripleurospermi sp. n. (Diptera: Cecidomyiidae), a new gall midge species on *Tripleurospermum perforatum* (Asteraceae: Anthemideae) in Europe, and a biological control agent in Canada

Marcela SKUHRAVÁ[1] & Hariet L. HINZ[2]

[1] Czech Zoological Society, Viničná 7, CZ–128 00 Praha 2, Czech Republic
[2] CABI Bioscience Switzerland Centre, Rue des Grillons 1, CH–2800, Delémont, Switzerland

Received November 6, 2000; accepted December 4, 2000
Published December 29, 2000

Abstract. *Rhopalomyia tripleurospermi* sp. n., causing galls on *Tripleurospermum perforatum* (Merat) Lainz (syn. *Matricaria perforata* Mérat) (Asteraceae: Anthemideae), is described and its taxonomically important structural features are illustrated. The new species is compared with several middle European congeners and taxonomical problems of the genus *Rhopalomyia* Rubsaamen, 1892 are discussed. Data about the biology and distribution of *R. tripleurospermi* sp. n. in Europe are given. It is a multivoltine species with potential for rapid population increase. It induces galls on all plant organs and all phenological stages of its host plant. *R. tripleurospermi* sp. n. develops exclusively on species of the genus *Tripleurospermum*, and was therefore selected as a biological control agent of *Tripleurospermum perforatum* in North America.

Taxonomy, new species, galls, biological control, distribution, Diptera, Cecidomyiidae, *Rhopalomyia*, Palaearctic region, Nearctic region

INTRODUCTION

Tripleurospermum perforatum (Mérat) Laínz. (syn. *Matricaria perforata* Mérat), is a plant species with common name "scentless mayweed", which is used in United Kingdom, and "scentless chamomile", which is used in North America. It belongs in the family Asteraceae (Compositae), tribe Anthemideae, and is a very common weed plant species in Europe. *T. perforatum* was accidentally introduced into North America at the end of the 19th century. In the last few decades it developed into a noxious and spreding weed of disturbed and agricultural land in the Canadian pairie provinces (Woo et al. 1991). Because chemical and cultural control methods often prove ineffective or uneconomical, a biological control project was initiated by the Canadian Ministry of Agriculture in 1990. The CABI Bioscience Switzerland Centre (former IIBC) in Delémont, Switzerland, was entrusted to search for host-specific phytophagous insect species associated with *T. perforatum* in Europe with the objective to introduce these as biological control agents into Canada. A search of the western European literature revealed 68 phytophagous insect species to be associated with *T. perforatum* (Woo et al. 1991), including two gall midge species, *Ozirhincus longicollis* Rondani, 1840 (syn. *O. chrysanthemi* (H. Loew, 1850), and *Rhopalomyia syngenesiae* (H. Loew, 1850) (Freese, 1990). During field surveys from 1990–2000, 25 phytophagous species were found on *T. perforatum*.

Galls on *Rhopalomyia tripleurospermi* sp. n. on *T. perforatum* were first discovered in southern Slovakia in 1972 (Skuhravá 1972), and then found again during one of the field surveys for potential biocontrol agents of *T. perforatum* in eastern Austria (Hinz 1993). According to keys of Houard (1908–1909), Rübsaamen & Hedicke (1925–1939) and Buhr (1964–1965), galls were initially identified to be caused by *Rhopalomyia hypogaea* (F. Löw, 1885), a gall midge that usually develops on wild chrysanthemums (H. Meyer in litt., H. Stelter in litt.). However, host-range investigations carried out at the CABI Bioscience Switzerland Centre in Delémont from 1995–1997 indicated that it is a different species, because development to adult of the gall midge was restricted to species in the genus *Tripleurospermum* (Hinz 1998). Detailed morphological investigations of adults, larvae and pupae by M. Skuhravá confirmed this assumption. Due to its restricted host-range, permission for field release of *R. tripleurospermi* sp. n. in North America was granted by the regulatory authorities in March 1999. Since its introduction it has established at several field sites in Canada and overwintered successfully (A. McClay pers. comm.).

In the present paper we give a detailed description of the morphological characters of *R. tripleurospermi* sp. n., compare it to several congeners, and discuss the taxonomic controversity concerning the genus *Rhopalomyia* Rübsaamen, 1892. In addition, we present some basic data on the distribution and biology of *R. tripleurospermi* sp. n. and on its suitability as a biological control agent. Detailed data of its biology and host specificity are given in Hinz (1998).

MATERIAL AND METHODS

In May 1995, galls of *Rhopalomyia tripleurospermi* sp. n. were collected from *Tripleurospermum perforatum* at a field site near Eisenstadt, Burgenland, eastern Austria, where galls had already been collected in 1993. Because *R. tripleurospermi* sp. n. is very rare in the field, a continuous rearing was established at the CABI Bioscience Switzerland Centre. Between 1995 and 1997, the life history and host-specificity of *R. tripleurospermi* sp. n. was investigated under semi-natural conditions in Switzerland and at field sites in eastern Austria. For a detailed description of methods used during experiments see Hinz (1998).

Larvae, pupae and adults of *Rhopalomyia tripleurospermi* sp. n., obtained during experiments in Switzerland, were preserved in 75% alcohol and sent to M. Skuhravá for identification and morphological studies.

For microscopic examination, specimens were mounted on slides either in Canada Balsam medium, in which case it was necessary to transfer specimens into 96%, 100% alcohol and xylene, or in Liquido Faure medium – specimens were then transferred directly from 75% alcohol into this medium. Morphological studies were made using a stereo-binocular microscope Amplival (Carl Zeiss, Jena, Germany) and drawings with the aid of a project microscope Visopan (Reichert, Austria, 1977).

For scanning-electron-microscope (SEM) examination, specimens were removed from 75% alcohol, transferred into 80%, 96% and 100% alcohol, then dehydrated in 100% acetone, critical point CO_2 dried (Pelco CPD2) and subsequently each specimen was mounted on a small metal stud. After sputter coating with gold (SEM coating unit Polaron E 5100) they were examined in JEOL JSM 6300 scanning electron microscope (Japan, 1992).

Terminology of morphological characters of adults, larvae and pupae of *R. tripleurospermi* sp. n. is according to Sylvén & Tastás-Duque (1993).

The holotype and paratypes of *R. tripleurospermi* sp. n. are kept in the collection of M. Skuhravá in the National Museum in Praha, Czech Republic.

The junior author is responsible for field observations and laboratory experiments, the senior author for determination and description of the new gall midge species.

TAXONOMY

Rhopalomyia Rübsaamen, 1892

Rübsaamen, 1892: 370.

TYPE SPECIES. *Oligotrophus tanaceticola* Karsch, 1879: 27 (designated by Kieffer 1896: 89).

Rhopalomyia (sensu lato) is a large, cosmopolitan genus including at present more than 160 described species in the world. More than 60 species occur in the Palaearctic region (Skuhravá 1984; Fedotova 1995a, b, 2000), 86 species in the Nearctic region (Gagné 1982, 1989), 9 species in the Neotropics (Gagné 1994), two species are known to occur in the Oriental region (Grover, 1972, 1981, Gagné 1973), and 5 species in Australasian and Oceanian region of which three seem to be native and two are immigrants from other parts of the world (Gagné 1989, Kolesík 1996, 1998). As far as we know, no species of this genus is known in the Afrotropical region (Harris 1980).

The conception of the genus changed in the course of the 20th century. Rübsaamen (1892) in establishing this genus gave the following diagnosis: "Claws simple, about as long as empodium; flagellomeres with whorls of hairs; male flagellomeres with longer stems, female flagellomeres with shorter stems. Wings with three veins, the third forked; fore wing margin with hairs. Palpi 1–2 segmented; hypopygium with strongly swollen dististylus." At the beginning of the 20th century seven genera were established which were distinguished from the genus *Rhopalomyia* by minor morphological characters as, for example, the number of palpal segments or the form of tarsal claws.

Gagné (1975) redefined the genus *Diarthronomyia* Felt, 1908 as a subgenus of *Rhopalomyia* and synonymized the genera *Panteliola* Kieffer, 1913, *Boucheella* Rübsaamen, 1915, *Navasiella* Tavares, 1919, and *Eudictyomyia* Tavares, 1920, under the genus *Rhopalomyia*. This conception has been followed in the *Catalogue of the Palaearctic Diptera* (Skuhravá 1986). Skuhravá (1997) included in the tribe Rhopalomyiini three genera, viz. *Dictyomyia* Tavares, 1919, *Misospatha* Kieffer, 1913, and *Rhopalomyia* Rübsaamen, 1892, the last genus with three subgenera: *Navasiella, Boucheella and Diarthronomyia.*

Fedotova (1999a,b, 2000) removed from synonymy the genera *Boucheella* and *Navasiella*, considering them as valid names, and established several new genera belonging to the tribe Rhopalomyiini based especially on morphological characters of pupae.

In the present paper the genus *Rhopalomyia* (sensu stricto) is characterized by the following combination of characters: reduced mouthparts with one-segmented palpi; male flagellomeres with long stems, female flagellomeres with short stems; R_5 meeting with costa nearly at the apex of wing; simple tarsal claws; gonostyli short, stout, with a large claw; ovipositor long, soft, not distinctly sclerotized; larvae without spatula sternalis and with reduced number of papillae and setae; pupae with strongly developed antennal horns and with a pair of facial horns; species forming galls usually on Asteraceae; pupation takes place inside galls.

***Rhopalomyia tripleurospermi* sp. n.**

(Figs 1–23)

TYPE MATERIAL Holotype male, Switzerland, Délemont, em August 1996, from galls on *Tripleurospermum perforatum*, population reared from galls originating from Austria, leg by Hinz, 1993 (type locality: Eisenstadt, Austria), slide number 7307 Paratypes 1 male, 2 females, 5 pupae, 6 larvae, same data; all in the collection of M. Skuhravá in the National Museum, Praha, Czech Republic

ADDITIONAL MATERIAL 10 males, 10 females, em. April 1997; 15 larvae, 5 pupae, April 1997, same data; deposited in the collection of M Skuhravá.

DIAGNOSIS. *Rhopalomyia tripleurospermi* sp. n. is a medium-sized gall midge species, 2.5–2.9 mm long, with holoptic eyes in both sexes, one pair of one-segmented, very small palpi, 2+14 segmented antennae and simple claws on all legs; the empodium longer than claws. The pupa has a pair of long, very strong, pointed antennal horns with a pair of strong spines at its base. Larva without spatula sternalis and body integument without structure. Larvae cause galls on *Tripleurospermum* spp. (Anthemideae).

Adult

DESCRIPTION. Male (Figs 1–3, 11, 17–20). Body size: 2.5–2.6 mm; wing length 2.3–2.7 mm, wing width 0.9–1.0 mm. Head and thorax dark brown, abdomen very slender and greyish coloured in fresh conditions. Head of normal size and position, with large holoptic eyes; eye bridge 5 ommatidia broad medially. Eyes with circular ommatidia. Mouthparts reduced. A pair of one-segmented palpi, the segment is ovoid, 30 µm long, densely covered with microtrichia and with several setae Palpiger absent Frontoclypeus with a group of thin, 50 µm long setae

Antennae 2+ 14 segmented, flagellomeres bottle-shaped, each except the last one with relatively long stem which forms about 1/3 of the length of the whole flagellomere Scape obconical, pedicel subglobular, both basal segments covered densely with microtrichia and with several setae, first and second flagellomeres fused Each flagellomere sparsely covered with microtrichia, with sensorial thread forming two incomplete rings which are connected with a connection and with a basal whorl of 60 µm long setae and with several 100 µm long setae which are inserted in large sensorial pores in the middle part of each flagellomere Terminal flagellomere is ovoid, rounded at the tip

Wings are slender, R_1 meeting with costa in the middle of anterior wing margin, R_5 slightly bent posteriorly and meeting with costa nearly at the apex of the wing, Cu in microscope slides indistinct

Legs very long and slender, densely covered with setae Claws simple on all legs, moderately bent, empodium a little longer than claws

Male terminalia gonocoxites thick, 170 µm long, 90 µm broad, densely covered with microtrichia, forming oblique rows on inner side, and with 75 µm long setae, gonostyli stout, ovoid, 100 µm long, 50 µm broad, densely covered with microtrichia and with sclerotized claw apically Mediobasal lobe (sheath of aedeagus) triangular, densely covered with hairs Cercus (upper lamella) heart-shaped, with shallow incision, hypoproct (middle lamella) deeply and broadly incised, shorter than cercus Aedeagus conical, as long as hypoproct.

Female (Figs 4–6, 10, 12–16) Body size 2 6–2 9 mm, wing length 2 3–2 4 mm, wing width 0 75–0 9 mm Abdomen bright red coloured in fresh condition Antennae 2+14 segmented, scape obconic, pedicel subglobular, both covered densely with microtrichia, flagellomeres cylindrical with short stems, terminal flagellomere acutely pointed Flagellomeres covered with microtrichia, each flagellomere with several sensorial hollows, with several 40 µm long setae and with a sensorial thread forming irregular cells Sensorial thread is very fine, hardly visible under optical microscope Frontoclypeus with a group of setae, each 40 µm long Palpus one-segmented, ovoid, 33 µm long, densely covered with microtrichia Ovipositor long, soft, before the end about 50 µm in diameter, cercus 50 µm long, densely covered with microtrichia and with several 10 µm long setae

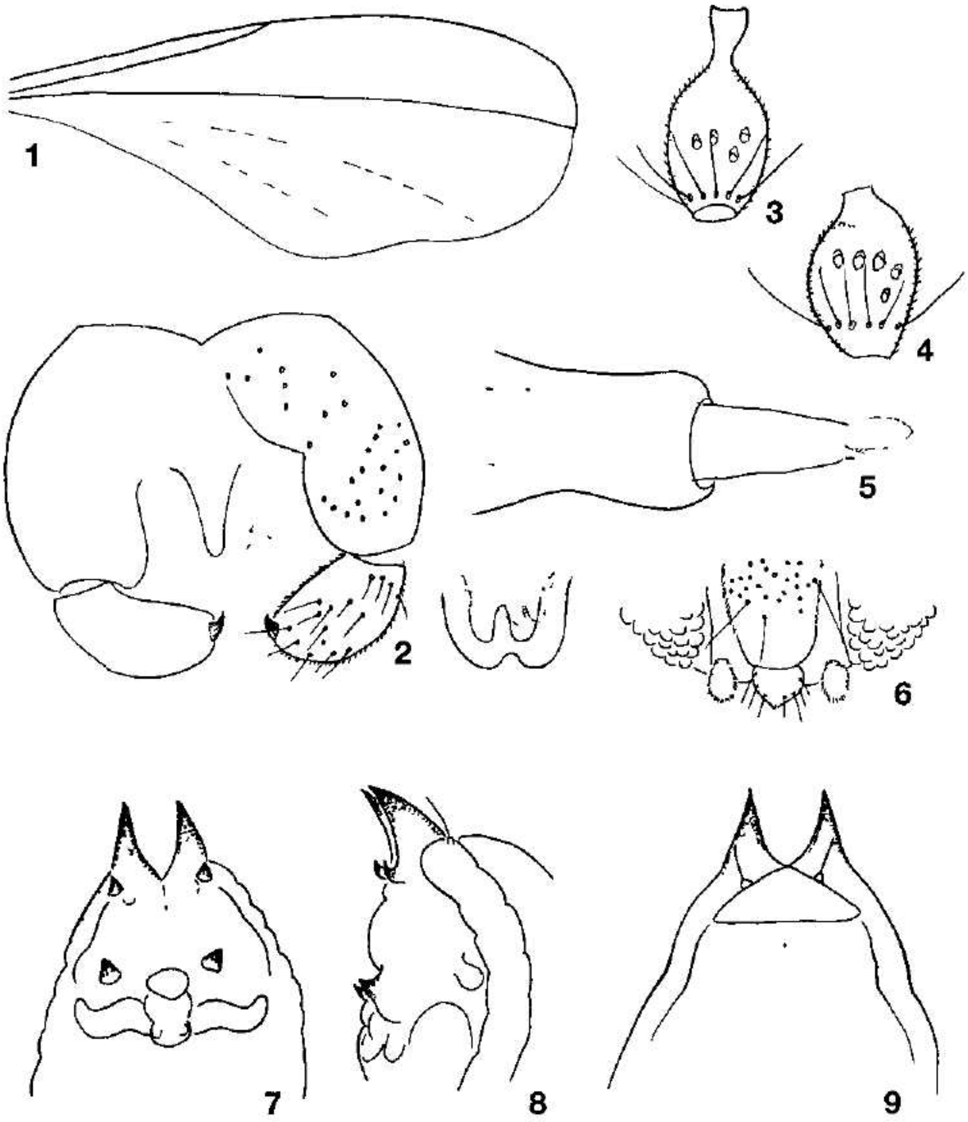
Adults of *Rhopalomyia tripleurospermi* sp n show sexual dimorphism in the size of the body, shape of abdomen, wings and legs Females have shorter and broader abdomen, wider wings, shorter and thicker legs than males Sexual dimorphism is also evident in the colour the female abdomen is red coloured, whereas the male abdomen is gray

DIFFERENTIAL DIAGNOSIS *Rhopalomyia tripleurospermi* sp n differs from the type species of the genus, *R tanaceticola* (Karsch, 1879), larvae of which cause galls on *Tanacetum vulgare* L , by the number of antennal segments *R tanaceticola* has 2+18, *R tripleurospermi* sp n only 2+14, the empodium of *R tripleurospermi* sp n is longer than the claws, whereas in *R tanaceticola* it is as long as claws, and by the shape of gonocoxites of male terminalia which are swollen on the inner side in *R tripleurospermi* sp n but unswollen in *R tanaceticola*

Rhopalomyia tripleurospermi sp n differs from *R syngenesiae* (H Loew, 1850), larvae of which live free among single flowers in the flower-heads of *Tripleurospermum maritimum* (L) Koch and *Anthemis arvensis* L without making galls (H Loew 1850), by the number of antennal segments *R syngenesiae* has 2+13 and *R tripleurospermi* sp n 2+14 *R hypogaea* (F Low, 1885) has the same number of antennal segments (2+14) as *R tripleurospermi* sp n , but larvae of *R hypogaea* cause subterranean galls on *Chrysanthemum atratum* Jacq (F Low 1885)

Egg

Eggs are bright red coloured, 0 32 mm long and 0 08 mm wide, and are adherent to the plant surface They are laid either singly, or in batches of 2–27 eggs



Figs 1–9 *Rhopalomyia tripleurospermi* sp n 1–6 adult, 7–9 pupa 1 – wing of male, 2 – hypopygium in ventral view showing aedeagus, cerci and hypoproct separated, 3 – 3rd flagellomere, male, 4 – 3rd flagellomere, female, 5 – ovipositor, 6 – mouthparts details, 7 – a part of pupa in ventral view, 8 – a part of pupa in lateral view, 9 – a part of pupa in dorsal view

Larva

The first instar larvae are red, the second and third instar larvae are white. Third instar larva is 2.5 mm long and 1 mm broad. Integument of ventral side is smooth, integument of dorsal side is formed by very small, pointed plates. Without spatula sternalis on the ventral side of the prothoracic segment. Terminal papillae usually irregular, with very short setae.

Pupa (Figs 7–9, 21–23)

Pupae are 2.5 mm long, 1.0 mm broad, greyish coloured in males and dark purple in females; head part, sheaths of wings, antennae and legs blackish brown. Male pupae are grey, female pupae dark purple. Integument of ventral and dorsal side of abdominal segments with many very small spinae. Basis of antennal sheaths with a pair of large, black, strongly sclerotized antennal horns directed obliquely forward. Antennal horns strongly developed, conical, 150 µm long, tapering gradually from base to pointed apex. A pair of subantennal horns, 30 µm long, at the base of antennal horts. Face with a pair of prominent, pointed facial protuberances which are situated above the palpal sheaths. A pair of cephalic papillae with 75 µm long cephalic setae. Prothoracic spiracle in the form of a small bulb.

NAME DERIVATION. The new gall midge species is named after the generic name of its host plant, *Tripleurospermum perforatum.* The genera *Tripleurospermum* and *Matricaria* are often used synonymously (Hegi, 1987). In our choice of a species name we followed the opinion of the Asteraceae specialist Prof. Dr. G. Wagenitz (University of Göttingen, Germany) and the nomenclature he suggested for the family Asteraceae (Wagenitz 1987).

BIOLOGY

Host plant

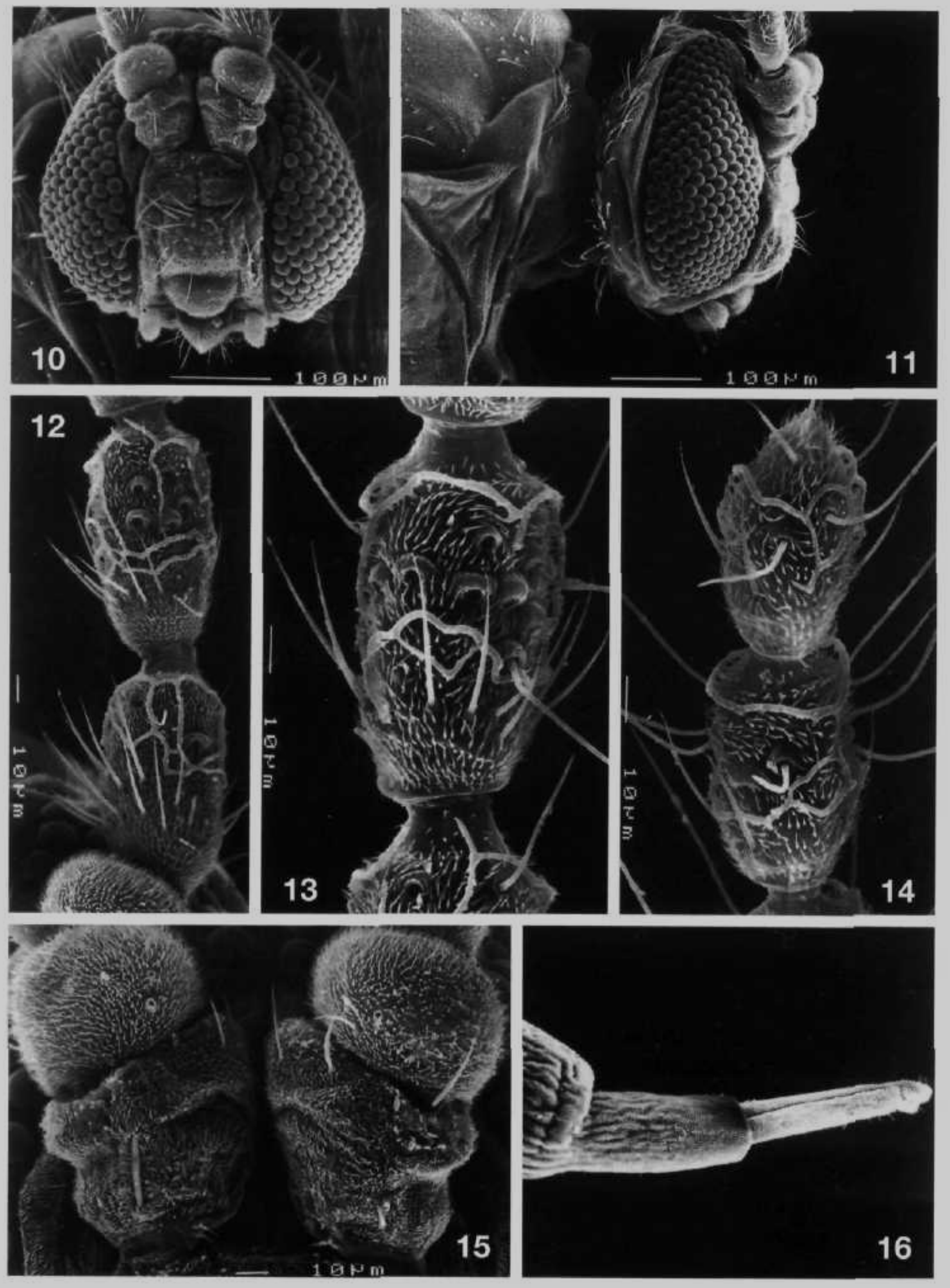
Rhopalomyia tripleurospermi sp. n. is restricted to host plants of the genus *Tripleurospermum* Fully-developed galls from which adults emerged were induced only on *Tripleurospermum perforatum* (Mérat) Laínz (syn. *Matricaria perforata* Mérat), on *T maritimum* (L.) Koch and on *T ambiguum* (Ledeb.) Franch. et Sav (Asteraceae). In the course of investigations in Switzerland, a total of 51 plant species and varieties of six tribes of the family Asteraceae were offered to females of *Rhopalomyia tripleurospermi* sp. n. for egg-lying. Development from egg to adults was restricted only to the host plants of the genus *Tripleurospermum*, and *T. perforatum* was the preferred host plant in all tests (Hinz 1999).

Gall

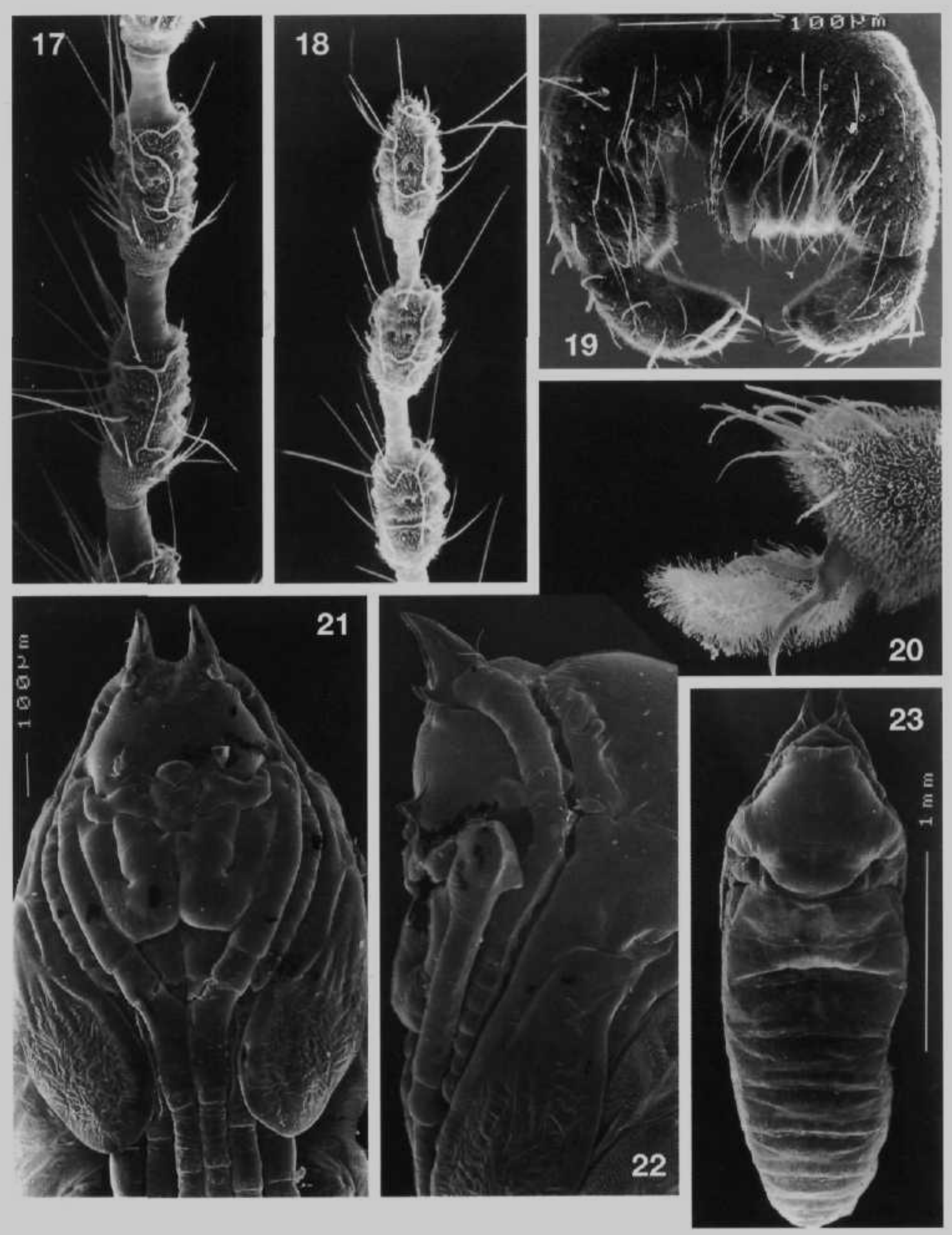
Galls of *Rhopalomyia tripleurospermi* sp. n. are induced in different meristematic tissues of *T. perforatum*, including the apical meristems of rosettes and bolting plants, leaf axils, buds and flower-heads Galls formed in axillary buds and flower-heads usually only consisted of one chamber, whereas the majority of galls induced in apical meristems consisted of several chambers, up to 80. Each chamber contains one larva. The size of galls increased with the number of chambers.

Life history

In Switzerland, *Rhopalomyia tripleurospermi* sp. n. has four generations per year in outdoor cages. Adults of the overwintering generation (considered to be the first generation) emerged at the end of March and in April, the second in June, the third in July/August, and the fourth in September/October. Depending on time of oviposition and temperature, larvae of different instars hibernate in galls and pupate the following spring. During summer, adults of the 2nd and 3rd generation emerge as early as 4.00 a. m. whereas in early spring and autumn adults of the 1st and 4th



Figs 10–16. *Rhopalomyia tripleurospermi* sp. n. 10 – head of female in frontal view; 11 – head of male in lateral view; 12 – 1st and 2nd flagellomeres of female; 13 – 3rd flagellomere of female; 14 – two terminal flagellomeres of female; 15 – scape and pedicel of female; 16 – ovipositor.



Figs 17–23. *Rhopalomyia tripleurospermi* sp. n. 17–20 male, 21–23 pupa. 17 – 1st and 2nd flagellomeres; 18 – three terminal flagellomeres; 19 – hypopygium; 20 – apical part of tarsus with simple claws and empodium; 21 – part of pupa in ventral view; 22 – part of pupa in lateral view; 23 – pupa in dorsal view.

generations emerge from around 7.00 a. m. After mating, females search for host plants which are suitable for oviposition.

Females contain all their eggs already upon emergence (proovigenic). One female contained on average 93 eggs (46–164). Females in culture produce an average of 61 offsprings, and the gall midge population may increase up to 150-fold during two generations. The adults of *R. tripleurospermi* sp. n. are short-lived; at constant 20 °C, females lived on average 16 hours and males 7 hours. The development from egg to adults at constant 25 °C took about 30 days, which is similar to the shortest time period observed for development during rearing.

Parasitism

In the field, galls of *Rhopalomyia tripleurospermi* sp. n. were attacked by one parasitoid species of the genus *Aprostocetus* Westwood, 1833 (Hymenoptera: Eulophidae). It is probably a new species to science (S. Vidal, pers. comm.). Parasitism ranged from 30–70%; the probability of parasitoid attack was higher in galls that consisted of several chambers, than in single-chambered galls.

Distribution

Rhopalomyia tripleurospermi sp. n. is a middle-European and Pannonian species with restricted area of distribution. It occurs in a small area of the most eastern Austria (close to the Hungarian border), northern Hungary and the most southern part of Moravia and Slovakia. Except for galls found near Eisenstadt (Hinz 1993), galls were also found at three localities situated along the southern boundary of Slovakia (Skuhravá 1972) and later at several other localities in southern Slovakia (Skuhravá 1991) and in Bohemia and Moravia (Skuhravá 1994 a,b), at Parndorfer Heide close to Zurndorf in eastern Austria (Skuhravá & Skuhravý 1995) and at Csobánka near Budapest in northern Hungary (Skuhravá & Skuhravý 1999). At these localities only one or two host plants attacked by *R.. tripleurospermi* sp. n. were found during faunal investigations. In the past, galls on *T perforatum* were found also in the Kamennaja Steppe near Voronezh, southern Russia (determined as *R hypogaea* F. Löw) (Dombrovskaja 1936). Recent data about the occurrence of *R. tripleurospermi* sp. n. at this locality are not at disposal.

R. tripleurospermi sp. n. seems to occur in its native range at very low population density. From the zoogeographical point of view, it is a rare species in the European gall midge faunas (Skuhravá 1987, Skuhravá & Skuhravý 1998, Skuhravá et al. 1984).

Biological Control

Due to its restricted host-range, permission for field release in North America was granted in March 1999. Since then, *R. tripleurospermi* sp. n. has established at several field sites in Canada and overwintered successfully (A. McClay pers. comm.).

Several life history traits are thought to make *R. tripleurospermi* sp. n. an effective biological agent. Impact studies have shown that *R. tripleurospermi* sp. n. reduces the height of plants and tends to reduce seed production (Hinz & Müller-Schärer 2000). *R. tripleurospermi* sp. n. is a multivoltine species with the potential for rapid population increase and it is independent of the availability of a particular phenostage of *T. perforatum*. Moreover, it is the only agent released so far that has the ability to attack and heavily damage the highly competitive overwintering overwintering rosettes of *T. perforatum*. Therefore, *R tripleurospermi* sp. n. is considered the most promising biological control agent for scentless chamomile (Hinz & McClay 2000).

Acknowledgements

The authors would like to express their thanks to Dr K. M Harris, Ripley, Woking, Surrey, UK, for his critical reading, advice and valuable comments on the manuscript. We are indebted to Prof G Wagenitz, Systematic-Geobotanical Institute, University of Göttingen, Germany, for his advice on the nomenclature of *Tripleurosper-*

mum perforatum We would also like to thank Dr H Meyer, Institute for Ecosystem Research and Ecological Technique, Christian-Albrechts-University Kiel, Germany, and Mr H Stelter, Friedland, Germany, for initial identification of *Rhopalomyia* Prof S Vidal, Institute for Plant Pathology and Plant Protection, Georg-August-University, Gottingen, Germany, kindly identified the parasitoid of *R tripleurospermi* sp n

We thank Dipl Ing Jana Nebesářova and Mr Antonin Polák, Laboratory of Electron Microscopy, Institute of Parasitology of Academy of Sciences of the Czech Republic, Česke Budějovice, for their technical help in preparing and taking the SEM photos

The junior author was funded by the Alberta research Council, Alberta Agricultural Research Institute, and Agriculture Development Fund (Saskatchewan)

REFERENCES

Buhr H 1964 1965 *Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen Mittel- und Nordeuropas* Jena VEB Gustav Fischer, 1572 pp

Dombrovskaja J V 1936 On the Cecidomyid fauna of the Kamennaja Steppe, USSR *Trav Inst Zool Acad Sci U S S R* 3 409–428 (in Russian, English summary)

Fedotova Z A *1995*a A review of Palaearctic gall-midges (Diptera, Cecidomyiidae) from Achillea and Tanacetum with description of three new species from Kazakhstan *Vestn Zool* **1995**(2–3) 22–33 (in Russian, English summary)

Fedotova Z A 1995b Review of gall midges (Diptera, Cecidomyiidae) damaging Aster and Erigeron in Kazakhstan Report 1 *Zool Zhurn* **74**(12) 44–58 (in Russian, English summary)

Fedotova Z A 1999a Gall midges (Diptera, Cecidomyiidae) developing on Artemisia taxa from Kazakhstan and Turkmenistan faunas The genera Bouchcella and Arenaromyia, gen n *Zool Zhurn* **78** 580–595 (in Russian, English summary)

Fedotova Z A 1999b Gall midges (Diptera, Cecidomyiidae) developing on Artemisia Fauna taxa of Kazakhstan and Turkmenistan 3 The genus Dracunculomyia, gen n *Zool Zhurn* **78** 834–848 (in Russian, English summary)

Fedotova Z A 2000 *Gallicy-fitofagi (Diptera Cecidomyiidae) pustyn i gor Kazahstana morfologia, biologia, rasprostranenie filogenia i sistematika* [*Gall Midges – Phytophags (Diptera, Cecidomyiidae) of Deserts and Mountains in Kazakhstan Morphology, Biology, Distribution and Systematics*] Samara Izd Samarskaja Gos Selskochoz Akad , 803 pp (in Russian)

Freese A 1990 Scentless chamomile (Tripleurospermum perforatum (Mérat) Lainz Work in Europe in 1990 *Annual Report, CAB International Institute of Biological Contral, Delemont, Switzerland*, 20 pp

Gagne R J 1973 Family Cecidomyiidae Pp 480–517 In Delfinado M D & Hardy D E (eds) *A Catalog of the Diptera of the Oriental Region Vol 1 Suborder Nematocera* Honolulu Univ Hawaii Press, 628 pp

Gagne R J 1975 A redefinition of Diarthronomyia Felt as a subgenus of Rhopalomyia Rubsaamen (Diptera Cecidomyiidae Oligotrophidi) *Ann Entomol Soc Amer* **68** 482–484

Gagne R J 1989a *The Plant-feeding Gall Midges of North America* Ithaca and London Cornell University *Press, 356 pp*

Gagné R J 1989b Family Cecidomyiidae Pp 152–163 In Evanhuis N L (ed) *Catalog of the Diptera of Australasia and Oceania* Honolulu Bishop Museum Press, 1155 pp

Gagne R J *1994 The Gall Midges of the Neotropical Region* Ithaca and London Cornell University Press, 352 pp

Grover P 1972 A revision of Indian Oligotrophini *Cecidol Ind* 7 1–29

Grover P 1981 A catalogue of Indian gall midges *Cecidol Internat* 2 63–108

Harris K M 1980 Family Cecidomyiidae Pp 238–251 In Crosskey R W (ed) *Catalogue of the Diptera of the Afrotropical Region* London British Museum (Natural History), 1437 pp

Hegi G 1987 *Illustrierte Flora von Mitteleuropa Spermatophyta* Berlin, Hamburg Paul Parey

Hinz H L 1993 Investigations on potential biocontrol agent of scentless chamomile (Tripleurospermum perforatum (Merat) Wagenitz) ***Annual Report, CAB International Institute of Biological Control, Delémont, Switzerland,*** 32 pp

Hinz H L 1997 *Rhopalomyia n sp (Diptera Cecidomyiidae), a candidate for the biological control of scentless chamomile in North America Final Report* Delemont International Institute of Biological Control, *European Station*, 16 pp

Hinz H L 1998 Life history and host specificity of Rhopalomyia n sp (Diptera Cecidomyiidae), a potential biological control agent of scentless chamomile *Environ Entomol* 27 1537–1547

Hinz H L & McClay A 2000 Ten years of scentless chamomile prospects for the biological control of a weed of cultivated land *Proc X Int Symposium of Biol Control of Weeds, 4–14 July 1999* Bozeman, Montana, USA

Hinz H L & Muller-Scharer H 2000 Influence of host condition on the performance of Rhopalomyia sp n (Diptera Cecidomyiidae), a biological control agent for scentless chamomile, Tripleurospermum perforatum *Biol Control* **18** 147–156

Houard C 1908–1909 *Les Zoocecidies des Plants d Europe et du Bassin de la Mediterranee* Paris A Hermann et Fils, 1247 pp

Kolesik P 1996 Rhopalomyia goodeniae, a new species of Cecidomyiidae (Diptera) damaging Goodenia lunata (Goodeniaceae) in inland Australia *Trans Roy Soc S Aus* **120** 155–160

Kolesik P 1998 Rhopalomyia lawrenciae, a new gall midge species (Diptera Cecidomyiidae) deforming leaves of Lawrencia squamata (Malvaceae) in South Australia *Trans Roy Soc S Aus* **122** 139–145

Loew H 1850 Dipterologische Beitrage Vierter Theil *Offentl K Friedrich-Wilhelms Gymnasium zu Posen* 1–40

Löw F 1885 Beitrage zur Naturgeschichte der gallenerzeugenden Cecidomyiden *Verh Zool -Bot Ges Wien* **35** 483–510

Rubsaamen H F 1892 Die Gallmucken des Konigl Museums für Naturkunde zu Berlin *Berlin Entomol Ztschr* **37** 319–411

Rubsaamen E H & Hedicke H 1925–1939 Die Zoocecidien, durch Tiere erzeugte Pflanzengallen Deutschlands und ihre Bewohner *Die Cecidomyiden (Gallmucken) und ihre Cecidien Zoologica, Stuttgart* **29**, Heft 77 1–350

Skuhravá M 1972 Gallmucken der Slowakei (Cecidomyiidae, Diptera) I Die Gallmucken der Mittleren Slowakei *Acta Rer Natur Mus Natl Slov Bratislava* **18** 21–67 (in Czech, German abstr)

Skuhrava M 1986 Family Cecidomyiidae Pp 72–297 In Soós A & Papp L (eds) *Catalogue of Palaearctic Diptera, Vol 4* Budapest Akademiai Kiado, 441 pp

Skuhrava M 1987 Analysis of areas of distribution of some Palaearctic gall midge species *Cecidol Internat* **8** 1–48

Skuhrava M 1991 Gallmucken der Slowakei (Cecidomyiidae, Diptera) VI Die Zoogeographie der Gallmucken *Zbor Slov Nar Muz , Prir Vedy* **37** 85–178

Skuhrava M 1994a The zoogeography of gall midges (Diptera Cecidomyiidae) of the Czech Republic I Evaluation of faunistic researches in the 1855–1990 period *Acta Soc Zool Bohem* **57**(1993) 211–293

Skuhrava M 1994b The zoogeography of gall midges (Diptera Cecidomyiidae) of the Czech Republic II Review of gall midge species including zoogeographical diagnoses *Acta Soc Zool Bohem* **58** 79–126

Skuhrava M 1997 Family Cecidomyiidae Pp 71–204 In Papp L & Darvas B (eds) *Contributions to a Manual of Palaearctic Diptera Vol 2 Nematocera and Lower Brachycera* Budapest Science Herald 592 pp

Skuhrava M & Skuhravy V 1995 Die Gallmucken (Cecidomyiidae, Diptera) von Osterreich II *Sitzungsber Osterr Akad Wiss Math -Nat Kl* **201** 3–34

Skuhrava M & Skuhravy V *1998* The zoogeographic significance of European and Asian gall midge faunas (Diptera Cecidomyiidae) Pp 12–17 In Csóka G , Mattison W J , Stone G , Price W (eds) The biology of gall inducing arthropods *Gen Tech REp NC 199*, St Paul, MN U S Dep Agr , Forest Service, North Central Research Station 329 pp

Skuhrava M & Skuhravy V 1999 Gall midges (Diptera Cecidomyiidae) of Hungary *Ann Histor-Natur Mus Natl Hung* **91** 105–139

Skuhrava M Skuhravy V & Brewer J W 1984 Biology of gall midges Pp 169-222 In Ananthakrishnan T N (ed) *Biology of Gall Insects* New Delhi, Bombay, Calcutta Oxford & IBH Publishing Company, 362 pp

Sylven E & Tastas-Duque R 1993 Adaptive, taxonomic and phylogenetic aspects *Zool Scripta* **22**(3) 277–289

Wagenitz G 1987 Nachtrage Berichtigungen und Erganzungen zum Nachdruck der 1 Auflage von Band VI/2 (1928/9) *Illustrierte Flora von Mitteleuropa, Spermatophyta Band VI, Angiospermae, Dicotyledones 4* Hegi G (Begr) Berlin, Hamburg Paul Parey

Woo S L , Thomas A G Peschken D P, Bowes G G , Douglas D W, Harms V L & McClay A S 1991 The biology of Canadian weeds 99 Matricaria perforata Merat (Asteraceae) *Can J Plant Sci* 71 1101–1119

Acta Soc. Zool. Bohem **64**: 437–445, 2000
ISSN 1211-376X

Karyotypes of some Central European mayflies (Ephemeroptera) *and their contribution to phylogeny of the order*

Tomáš SOLDÁN[1] & Milan PUTZ[2]

[1] Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31,
CZ-370 05 České Budějovice, Czech Republic
[2] Faculty of Biological Sciences, University of South Bohemia, Branišovská 31,
CZ-370 05 České Budějovice, Czech Republic

Received March 22, 1999, accepted December 3, 2000
Published December 29, 2000

Abstract. Based on study of larval spermatocytes the karyotypes of 24 species of 16 genera and 9 families of Central European Ephemeroptera have been described in addition to 8 species previously mentioned in literature. Karyotypes of the families Siphlonuridae, Oligoneuriidae, Leptophlebiidae and Potamanthidae are mentioned for the first time. The species studied represent all major recent phylogenetic lineages within the order. In general, the Ephemeroptera show karyotypes with a range of n = 4–10 chromosomes with unclear modal number and two types of sex determination (XY/XX and X/XX, males heterogametic). Anagenetic trends forming karyotypes in individual families are suggested. Plesiomorphic line (Siphlonuridae–Baetidae) is characterized mainly by still relatively high number of acrocentric chromosomes and XY/XX sex determination. Derived lines show various transitions to submetacentric and metacentric chromosomes, changes in chromosome numbers (mostly reduction) and, finally, the emergence of X/XX sex determination type in the advanced Ephemeridae and Caenidae. Parsimonial hypothetical scheme of karyotype anagenesis suggested here mostly corresponds to results obtained by study of external and internal morphological structures. Relations of the mayfly karyotype to that of the Odonata, a phylogenetically most allied order, are discussed. Quite different Ephemeroptera karyotype supports the idea of the Ephemeroptera and Odonata + Neoptera sister grouping of pterygote insects.

Chromosome numbers, sex determination, chromosome anagenesis, phylogeny, pterygote insect clades, higher classification, Ephemeroptera

INTRODUCTION

Study of karyotypes and cytogenetical study in general may bring a new insight on insect taxonomy and classification. This becomes apparent e. g., in Lepidoptera and Diptera where quite new opinions concerning higher classification are being currently formulated. On the other hand, the order Ephemeroptera is largely omitted in this respect and our present knowledge is very scarce and rather fragmentary.

Of the 25 families and more than 4,000 species described so far (Hubbard 1991), the chromosome numbers are known only in 8 species of 4 families. Bernhard (1907) first studied the karyotype of *Cloeon dipterum* (Linné, 1761) (Baetidae). He found a haploid chromosome number of n=5 in oocytes of this species. The same chromosome number was found in oogenetic and cleavage stages of the same species by Wolf (1960) who first mentioned the sex determination in mayflies (XY/XX, males heterogametic). Identical chromosome numbers and type of sex chromosome determination were observed in both oocytes and spermatocytes of *Baetis rhodani* Pictet, 1843 and *B. vernus* Curtis, 1834 (Baetidae) by Bohle (1969). Katayama (1939) published the karyotype of *Ameletus costalis* (Matsumura, 1931) (Ameletidae) (n=9) and found the same type of sex determination as in Baetidae (XY/XX, males heterogametic). However, Wolf (1946) and Mol (1978) observed a derived sex chromosome system, X/XX in *Ephemera danica* Muller, 1764 (missing Y chromosome in males), (2n=11 in males, 2n=12 in females) The system X/XX was also found in *Caenis horaria* (Linne, 1758) (Caenidae), whereas *Serralla ignita* (Poda, 1761) (Ephemerellidae) and *Ecdyonurus dispar* (Curtis, 1834) (Heptageniidae) possessed the XY/XX system like the family Baetidae (Mol 1978) Kiauta & Mol (1978) described the whole development of spermatocyte chromosomes and suggested a very simple phylogenetic relationships within the order comprising two basic lineages defined mainly by the sex determining system According to the karyotype arrangement they distinguished the heptagenioid line comprising the families Ameletidae and Baetidae (higher chromosome number, XY/XX sex determination) on one side and ephemeroid line (lower chromosome number X/XX sex determination) on the other Updated knowledge on karyotypes of 7 species occurring in Austria was summarized by Humpesch & Elliott (1984)

The objective of this study is to describe, on the basis of Central European species, chromosome numbers and type of sex determination of all major stem groups within the order and reconstruct possible anagenesis of the Ephemeroptera karyotype In addition, we have compared the Ephemeroptera karyotype with that of Odonata in order to contribute to the discussion on definition of major clades of pterygote insects

MATERIAL AND METHODS

Karyotypes of the following species have been studied (all the material collected by senior author in the Labe basin Czech Republic, coordinates of localities according to the uniform grid system) (see e g , Buchar 1982)

Siphlonuridae *Siphlonurus lacustris* (Eaton, 1870) Modravsky brook, Modrava (7046), September 7, 1995

Baetidae *Baetis alpinus* (Pictet, 1843) Krasetinsky brook, Krasetin, (7151), April 6, 1996, *B rhodani* (Pictet 1843) Kličava brook, Zbečno (5949), August 14, 1995, *B vernus* Curtis, 1834 Malše river, Kaplice (7252) August 1, 1995, *Centroptilum luteolum* (Muller, 1776) Malše river, Kaplice (7252), August 1, 1995, *Nigrobaetis niger* (Linne, 1761) Vltava river, Větřni (7251), April 17, 1996

Heptageniidae *Ecdyonurus austriacus* Kimmins, 1958 Zhůřsky brook (tributary of the Vydra river), Turnerova chata (6947), June 15, 1995, *E subalpinus* Klapalek, 1905 small unnamed brook Rakovnik (5848), March 23, 1996, *E submontanus* Landa 1970 Blanice river, Blažejovice (7049), August 1, 1996, *E torrentis* Kimmins, 1942 Vltava river Třisov (7152) August 6 1996, *Electrogena fascioculata* (Sowa, 1974) Oupořsky brook, Skryje (6048) August 15 1995, *Epeorus sylvicola* (Pictet, 1865) Vltava river, Větřni (7251), April 17, 1996 *Heptagenia flava* Rostock 1877 Malše river, Kaplice (7252), August 1, 1995, *H sulphurea* (Muller, 1776) Malše river Kaplice (7252), August 1 1995, *Rhithrogena savoiensis* Alba-Tercedor et Sowa, 1987 Malše river, Pořešin, August 8, 1995 *R semicolorata* (Curtis, 1834) Kleštinsky brook, Čertova stěna (7351), April 17, 1996

Oligoneuriidae *Oligoneuriella rhenana* (Imhoff, 1852) Malše river, Kaplice (7252), July 10, 1995

Leptophlebiidae *Habroleptoides confusa* Sartori et Jacob, 1986 Kličava brook, Lany (5849), March 25, 1996 *Paraleptophlebia submarginata* (Stephens 1835) Křemžsky brook, Holubov (7051), April 6, 1996

Caenidae *Caenis macrura* Stephens, 1835 Křemžsky brook, Holubov (7051), August 10, 1995

Ephemerellidae *Ephemerella mucronata* Bengtsson, 1909 Krasetinsky brook, Krasetin (7151), April 10, 1996

Ephemeridae *Ephemera danica* Muller, 1764 Pšovka river, Kokořin (5553) April 1 1996 *E lineata* Eaton 1870 Nova řeka river, Mlaka (6955) June 10, 1995, *E vulgata* Linne, 1758 Pšovka brook, Kokořin (5553), April 1 1996

Potamanthidae *Potamanthus luteus* (Linne, 1767) Berounka river, Skryje (6048), August 15, 1996

Larvae of species studied were collected by usual hydrobiological techniques (kicking techniques, sweeping of submerged vegetation, individual collecting from larger stones etc) Since the number of larval instars cannot be properly determined in mayflies and this number varies even within the same population we used so called "older larvae", i e those with fully developed larval characters, several instars before the subimaginal moulting This appears to be an optimal stage of larval development since both spermatocytes and oocytes undergo meiotic division just in these instars Later (in the last and last but one instars) mostly spermatids and mature spermatozoa occur in male larvae and vitellogenesis is nearly finished in female ones (Soldan 1979a, 1979b)

To study chromosome numbers, fresh generative tissues of gonads were used Larvae of both sexes were studied but we preferred to determine spermatocyte chromosome numbers since oocyte chromosomes are mostly superimposed by yolk granules and their counting is more difficult We followed essentially the procedure described in

Traut (1976). Specimens were dissected in a physiological saline, gonadal tissues were fixed for 5 minutes with the Carnoy fixative then disintegrated with wolfram needles on microscopic glasses and macerated for several minutes with 60 % acetic acid at 45 °C. After drying up preparations were stained with lacto-acetic-orcein, embedded and observed under Jenalumar (Karl Zeiss Jena) and Leitz Orthoplan microscope. Photographs were taken by the Expomet apparatus under oil immersion 100x objective. In addition, squash preparations were made as well and the fluorescent dye DAPI was used for staining chromosomes of unfertilized eggs (e. g., in *Baetis alpinus* and *Ecdyonurus subalpinus*). In the latter case, the fluorescence microscope Jenalumar was used.

RESULTS

In *Siphlonurus lacustris*, the only representative of the Siphlonuridae studied, the karyotype of 2n (male) = 16+XY was found. At spermatogonial metaphase, a rosette of 18 relatively small acrocentric chromosomes of nearly the same length was observed (Fig. 1A).

Within the family Baetidae, a uniform chromosome number, 2n (male) = 8+XY and 2n (female) = 8+XX, was found in all 4 genera studied. Correspondingly, 10 chromosomes observed in *Baetis alpinus* spermatogonia, one of couplets being apparently smaller (Fig. 1B). The chromosomes of the same species are well separated and much longer in late mitotic prophase of the same species. Chromosomes of *B. vernus* and *B. rhodani* seems to be microscopically identical with those of *B. alpinus* and *Centroptilum luteolum*. Contrary to *B. alpinus*, 10 acrocentric chromosomes of approximately the same length were observed in *Nigrobaetis niger* (Fig. 1C).

All the material of the Heptageniidae studied (9 species, 5 genera) shows the same chromosome numbers and sex determination type, 2n (male) = 18+XY and 2n (female) = 18+XX. Chromosomes of the Heptageniidae are very small in comparison with those of the Baetidae, equal in size and length but relatively short. At late diakinesis, ten elements can be found in the male, one of them being slightly asymmetrical. Their length in metaphase is only about 2–3 times longer than width as seen e. g., in 20 approximately identical chromosomes in metaphase of spermatogonia of *Rhithrogena semicolorata* or *Epeorus sylvicola*. Chromosomes of this group are submetacentric, in contrast to Siphlonuridae and Baetidae. Submetacentric chromosomes and the same type of sex determination were found also in the family Oligoneuriidae. Chromosomes are very small and equal in length as in Heptageniidae but their number is by two chromosome pairs lower, 2n (male) = 14+XY.

Although we studied only a single representative of the Ephemerellidae, *Ephemerella mucronata*, with 2n (male) = 6+XY and 2n (female) = 6+XX, karyotype of this family seems to show some peculiar characters. Mitotic metaphase clearly shows 2 large metacentric chromosomes and 6 smaller acrocentric ones (Fig. 1D). Large chromosomes are V-shaped and approximately double-sized, others are more or less rod-shaped.

As to the family Leptophlebiidae, we failed to determine proper chromosome number and type of sex determination. Size of chromosomes in both species studied, *Habroleptoides confusa* and *Paraleptophlebia submarginata* is extremely small (probably due to minute spermatozoa size) not permitting either to count their number or to find heterochromosome under the light microscope. Although we cannot define it with certainty, we estimate the chromosome number of both these species as follows: 2n (male) = 12–14.

The genus *Ephemera* Linné, 1758 was the only representative of the Ephemeridae studied. Surprisingly, different karyotypes have been found within this genus: 2n (male) = 10+X (*E. danica* and *E. lineata*) and 2n (male) = 12+X (*E. vulgata*). Thirteen chromosomes, two of them with apparent negative heteropycnosis were observed in the latter species (Fig. 1E).

Like in the Ephemeridae, also in the Potamanthidae (*Potamanthus luteus*) and Caenidae (*Caenis horaria*) a different type of sex determination, 2n+X (male heterogametic) has been found. The same autosome number (2n = 6) occurs in both these species studied. In *P. luteus*, there are 3 bivalents in pachytene and unclear, positively stained pycnotic formation most probably representing the X chromosome (Fig. 1F). Apparently differentiated 7 metaphase chromosomes were observed in *C. macrura*.

DISCUSSION AND CONCLUSIONS

Comparison of results with literature data

Our results generally agree with literature data. We would like only to emphasize, contrary to e. g., Mol (1978), that the last larval instar ("ultimate stage of larvae") can hardly be used to study mayfly karyotypes, at least in males. In this instar, all generative cell are in the stage of spermatids, presperms or even mature spermatozoa, meiotic division is completely finished and chromosomes mostly not discernible at all. Both spermatogenesis and oogenesis in mayflies are realized in only a single way and are completely finished before larval-subimaginal ecdysis, perhaps except the species with relatively long-term subimaginal stages like e. g., *Ephemera danica* (Soldán 1979a). Based on a description of meiotic spermatocytes (Kiauta & Mol 1977) probably last but one or earlier instars were used anyway. However, this study can be conducted in females since meiosis is mostly not finished before fertilization (cf. Soldán 1979c) although counting chromosomes is very difficult due to high content of yolk granules.

The Ephemeroptera karyotypes seem to be very similar each other at least at the family level. For instance, within the family Baetidae, we found the same chromosome numbers 2n=10 not only in the genera *Baetis* Leach, 1815 (cf. Bohle 1969) and *Cloeon* Leach, 1815 (cf. Bernhard 1907, Wolf 1960, Kiauta & Mol 1977) but also in *Nigrobaetis* Novikova & Kluge, 1987 and *Centroptilum* Eaton, 1869. Moreover, these genera represent relatively remote phylogenetic lines (different subfamilies) within this group. The same applies to the Heptageniidae, identical karyotype occurs at least in 5 genera mentioned in this study (same karyotype found also by Mol 1978 for *Ecdyonurus dispar*). Within the superfamily range, the karyotype seems to be similar in related families as seen in Siphlonuridae and Ameletidae (same chromosome number in the latter described by Katayama 1939 for *Ameletus costalis*). However, different chromosome numbers evidently occur in different lines at this hierarchic level (Siphlonuridae vs. Baetidae or Heptageniidae vs. Oligoneuriidae).

The only exception of this rule known so far is genus *Ephemera* (Ephemeridae). While the karyotype $2n = 10+X$ was found in *E. danica* (cf. Wolf 1946, Mol 1978) and also in *E. lineata*, *E. vulgata*, although closely related, apparently showed the male karyotype of $2n = 12+X$. Although we have nearly no data concerning the same genus in advanced families, this might indicate some more detailed karyotype differentiation in this group of mayflies. On the other hand the karyotypes of *Caenis horaria* and *C. macrura* are identical (cf. Mol 1978).

General features of the Ephemeroptera karyotype and comparison with the order Odonata

Generally, there are three theoretical possibilities of sister grouping of the Pterygota: (1) monophyly of Paleoptera, (2) monophyly of Ephemeroptera + Neoptera, and (3) monophyly of Odonata + Neoptera (see e. g., Kukalova-Peck 1991, Kristensen 1981 and Soldán 1997 for details). However, the proper reconstruction of phylogeny and higher classification of pterygote insects remains still open due to numerous contradictions and disputable circumstances concerning extant representatives. Many authors (e. g., Matsuda 1981, Kukalova-Peck 1983, Riek & Kukalova-Peck 1984 and Pfau 1986) believe that the views of recent dissenters cannot be reconciled with modern systematic arguments. Consequently, all major pterygote clades can be treated as independent groups, three paleopterous (ephemerids, odonatoids and the paleozoic plant-sucking paleodictyopteroids) and one neopterous.

Within the frame of this considerations, the comparison of the Ephemeroptera on one hand and the Odonata on the other hand seems to be the main source of knowledge. Although only 24 species of 9 families in Ephemeroptera contrary to about 500 species of 22 families of Odonata (Kiauta 1972) are known from the cytogenetic point of view genotypes of these to orders exhibit very remote similarities. The Ephemeroptera possess monocentric chromosomes, whereas chromosomes of Odonata are holokinetic (cf. Kiauta & Mol, 1977). Chiasmatic meiosis occurs in both sexes in both Ephemeroptera and Odonata but the recombination indices (RI) are different. In Ephemerop-

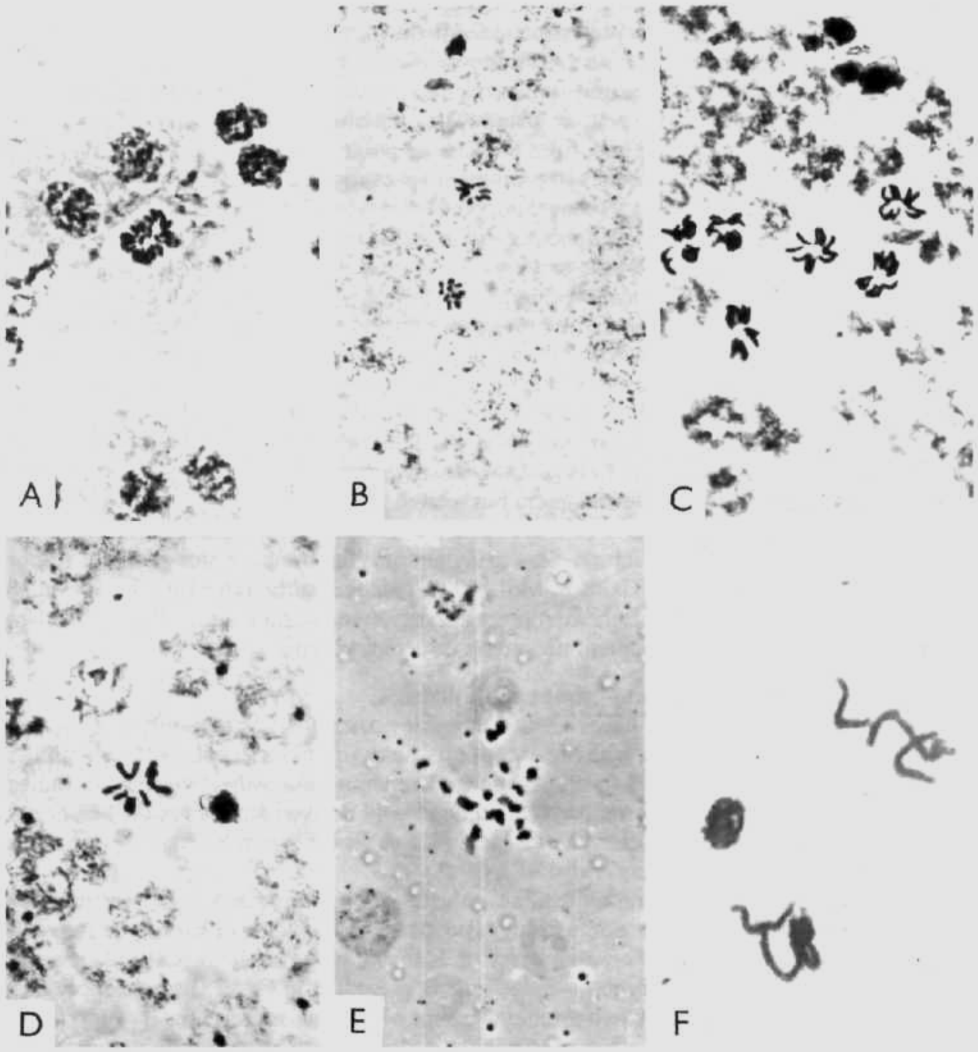


Fig. 1. Chromosomes of generative testicular cell of some species of Central European Ephemeroptera. A – spermatogonial metaphase of *Siphlonurus lacustris* (Eaton). B – late mitotic prophase of *Baetis alpinus* Pictet spermatocyte. C – spermatogonial metaphase of *Nigrobaetis niger* (Linné). D – mitotic metaphase of *Ephemerella mucronata* (Bengtsson) spermatocyte. E – metaphase of *Ephemera vulgata* Linné male generative cell. F – pachytene in spermatocytes of *Potamanthus luteus* (Linné).

tera, the are probably $2n < RI < 3n$, RI $2n$ in female of XY/XX sex determination species while $RI = 2n - 1$ in females of Odonata (in primary complements only). Chromosomal numbers widely vary in different families of Ephemeroptera, in the range of $n = 3$–9 in so far known species. Hence, their type number is uncertain. In Odonata, the type number is $n = 13$ with range of 9–14 (in primary complements only). Sex determination also differs in Odonata and Ephemeroptera. While the X/XX system exclusively was found in the former, the Ephemeroptera possess either XY/XX or X/XX systems. Males are heterogametic in both Ephemeroptera and Odonata although the sex element(s) are prereductioned in the former but postreductioned in the latter (Kiauta & Mol 1977). Moreover, karyotypes in Ephemeroptera differ at the family or even higher level (in Neoptera usually at generic or lower level) and chromosome numbers represent at most 2.5 multiplication of lowest number observed. Provided that chromosome multiplication by mutations mostly occur in derived taxa, the Ephemeroptera can be ranged, from the general point of view, to very primitive groups. This well agree with the general absence of prominent apomorphies in this order.

To conclude, the above arguments seem to support the monophyly of Odonata + Neoptera and their respective sister-grouping to the Ephemeroptera seems to be parsimonial although morphological autapomorphic of mayflies (sliding articulation of mandibles, arrangement of tentorial muscles, presence of true hypopharyngeal superliguae, prominent basal subcostal brace and terminal filament in larvae, retention of subimaginal stage etc.) are not so obvious, contrary to prominent ordinal autapomorphies of the Odonata. This sister-grouping is also supported by some recent ultrastructural findings, like presence of the telotrophic type of ovarioles (Gottanka & Büning 1992), spermatozoa with a unique 9+9+0 axoneme pattern and only a single mitochondrial derivative (Baccetti et al. 1969) and presence of very derived, extraordinarily small spermatozoa without flagellum (Soldán 1979b). Wheeler (1989) demonstrated that sequences of bases in the ribosomal DNA are quite different in the Ephemeroptera but related in Odonata + Neoptera. Moreover, the karyotype of Ephemeroptera seems to be more related to that of Archaeognatha, at least as far as the chromosome numbers are concerned, than to Zygentoma, a possible sister-group of ectognathous, true insects (Argilas 1941, Kiauta & Mol 1977). This fact, although a little irrelevant, also stresses the unique position of the Ephemeroptera karyotype in relation to that of Odonata which is apparently more related to the general neopteran insect karyotype.

Karotype constitution of major stem-groups of the order

In spite of only 9 families studied here our model species cover the whole family-level range of extant representatives of the order, with the exception of extralimital tricorythid-leptohyphid and prosopistomatid-baetiscid lines the karyotypes of which remains unknown. However, all studies of phylogeny of the order suppose these lineages to be clearly derived from caenid-like ancestors (Edmunds 1972, Edmunds & McCafferty 1979, Landa & Soldán 1989, McCafferty 1991) the idea of karyotype similarity seems to be very realistic.

Taking into account, with certain objections, general apomorphic karyotype constitution defined by Kiauta & Mol (1977) we are able to suggest parsimonial scheme of karyotype anagenesis and to discuss it with respect to the opinion based on both external morphological and anatomical study. Hypothetical scheme of karyotype anagenesis is presented in Fig. 2. Based simply on the type of sex determination, there are two principal groups of families represented by superfamilies Siphlonuroidea (and/or Heptagenioidea + Leptophebioidea) on one hand and Ephemeroidea and Caenoidea (possibly plus Prosopistomatoidea) on the other. We suggest the following anagenetic trend to form the karyotype of the above main stem groups: (1) Provided that metacentric chromosomes arose from acrocentric ones by Robertsian fusion, mayfly acrocentric chromosomes (plesiomorphic) gradually changed to submetacentric and then to metacentric ones (apomorphic), (2) autosome numbers are gradually reduced (highest numbers in the Ameletidae and Siphlonuridae plesiomorphic), at first in a lesser degree that substantially and their size gradually increases (apomorphic), and (3) reduction of the non-homological chromosome (presence plesiomorphic) gradually takes place, XY X (missing heterochromosome apomorphic).

The plesiomorphic line of the order (classified as the suborder Pisciformia by McCafferty 1991) and generally including schistonotan families (for definition see McCafferty & Edmunds 1979) with fish-like larvae is characterized by still high number of acrocentric chromosomes as seen in the Ameletidae (Katayama 1939) and Siphlonuridae (Fig. 2). Smaller number of chromosomes in extremely diversified world-wide family Baetidae (identical in both major subfamilies, Baetinae and Cloeoninae) can be explained by possible secondary reduction, taking into consideration half chromosome number and double size in comparison with the Siphlonuridae/Ameletidae. First of all, some speculations on permanent blocking of homeotypic meiotic division or endomitosis might be taken into account.

Evident sister groups, the Heptageniidae and Oligoneuriidae (superfamily Heptagenioidea in higher classification by Edmunds & McCafferty 1979 and Landa & Soldán 1989, suborder Setisura in that by McCafferty 1991) are characterized by evident plesiomorphy in the chromosome number and apomorphy in the centromere position (chromosomes submetacentric). The latter character seems to be important since a secondary multiplication of originally reduced chromosome number (see evidently smaller chromosome size in comparison e. g., with Siphlonuridae) might occur.

From the karyotype arrangement point of view, clearly derived (apomorphic) line of the order is represented by the families Ephemeridae and Caenidae within our model groups (Fig. 2). This line is characterized, first of all, by different type of sex determination (XX/X, males heterogametic). Especially the largely accepted superfamily Ephemeroidea containing, besides the Ephemeridae and Potamanthidae studied here further 4 families characterized by specialized burrowing larvae

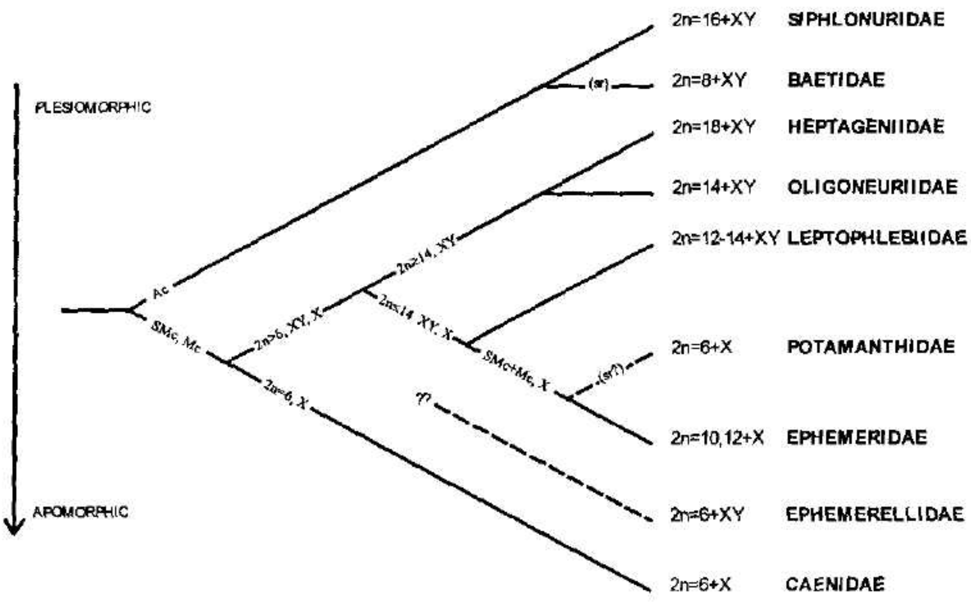


Fig. 2. Hypothetical scheme of karyotype anagenesis of the Ephemeroptera. Ac – acrocentric, SMc – submetacentric, Mc – metacentric chromosomes, (sr) – possible somatic reduction of chromosomes

and other characters (Landa & Soldán 1989, McCafferty 1991) seems to be very well defined by its karyotype. However, the genus *Ephemera* is the only known case showing different karyotype at generic level (see above). Although we were not able to determine the chromosome number of the family Leptophlebiidae perfectly, this family belongs to this line as well. Despite probably XX/XY sex determination type, its chromosomes are still metacentric and due to their extremely small size seem to be very derived. Their size can be documented e. g. by an extremely small size of spermatozoa reaching only 2–4 µm in diameter (Soldán 1979b), the smallest size within the whole animal kingdom. Consequently, we classify this family within the ephemeroid line as a transitory type from the cytogenetic point of view. McCafferty (1991) classifies the Leptophlebiidae and Ephemeroidea in the suborder Lanceolata. However, differentiation of karyotypes seems to be very old, taking into account different type of sex determination and differences in position of centromere.

The only family of those studied here, Ephemerellidae, does not fit to conventional classification as far as its karyotype is concerned. According to recent opinions (Edmund & McCafferty 1979, Landa & Soldán 1989, McCafferty 1991) the Ephemerellidae constitute a sister-group to the Caenidae with respect to derived characters of thoracic nota and abdominal segments, arrangement of gills, centralization of ventral nerve cord, reduction of visceral tracheae etc. Consequently, the Ephemerellidae are currently classified within the suborder (or infraorder) Pannota. This does not concern the chromosome number itself – in this case it is lower than in the ephemeroid lineage and higher than in the Caenidae. However, both acrocentric and metacentric chromosomes have been found in the genus *Ephemerella* and XX/XY sex determination type apparently separates this group out from the clearly pannotan, caeniod lineage. Being strictly formal in construction of our scheme (Fig. 2) we are not able to properly root the family Ephemerellidae with the pannotan stem-groups. Although more detailed cytogenetic study of other genera is urgently needed, this contradiction might be explained by some type of retention of rather primitive karyotype. This hypothesis is supported by the fact that this family represent the most primitive lineage of caenoid group showing evident relationships to schistonotan groups.

Acknowledgement

Our sincere thanks are due to Dr František Marec of the Institute of Entomology in České Budějovice for encouragement, critical reading of manuscript and valuable comments.

REFERENCES

ARGILAS A 1941 *Contribution à l'étude de Dilta littoralis Wom (Thysanure Machilidae)* Bordeaux. Thése , 226 pp

BACCETTI B , DALLAI R & GIUSTI F 1969 The spermatozoa of the Arthropoda. VI Ephemeroptera *J Ultrastruct Rev* **29** 343–349

BERNHARD C 1907 Uber die vivipare Ephemeride Cloeon dipterum *Biol Zbl.* **27** 467–479

BOHLE H W 1969 Untersuchungen uber die Embryonalentwicklung und die embryonale Diapause bei Baetis vernus Curtis und Baetis rhodani (Pictet) (Baetidae, Ephemeroptera) *Zool Jb Anat* **86** 493–475

BUCHAR J 1982 Publication of faunistic data from Czechoslovakia *Věst Čs Společ Zool* **46** 317–318.

GOTTANKA J & BUNING J 1992 Mayflies (Ephemeroptera) the most "primitive" winged insects, have telotrophic meroistic ovaries *Arch Dev Biol* **203**. 18–27

HUMPESCH U H. & ELLIOTT J M 1984. Zur Okologie adulter Ephemeropteren Österreichs. *Arch. Hydrobiol* **101**· 179–207

KATAYAMA H 1939 The sex chromosomes of a mayfly Ameletus costalis Mats. (Ephemerida) *Jap J Genet* **15** 139–144.

KIAUTA B 1972 Synopsis of the main cytotaxonomic data in the order Odonata *Odonatologica* **1**· 73–102.

KIAUTA B. & MOL A W. M 1977 Behaviour of the spermatocyte chromosomes of the mayfly, Cloeon dipterum (Linneaus, 1761) s. l. (Ephemeroptera, Baetidae), with a note on the cytology of the order *Genen Phaenen* **19**: 31–39

Kristensen N P 1981 Phylogeny of insect orders *Ann Rev Entomol* **26** 135–157

Kukalova-Peck J 1991 Fossil history and evolution of hexapod structures Pp 141–179 In Naumann I D (ed) *The Insects of Australia* Carlton CSIRO, Melbourne Univ, 1139 pp

Kukalova-Peck J 1983 Origin of the insect wing and wing articulation from the arthropodan leg *Canad J Zool* **61** 1618–1669

Landa V & Soldan T 1985 *Phylogeny and higher classification of the order Ephemeroptera A discussion from the comparative anatomical point of view Studie ČSAV 4* Praha Academia, 121 pp

Matsuda R 1981 The origin of insect wing (Arthropoda, Insecta) *Internat J Morphol Embryol* **10** 387–389

McCafferty W P 1991 Toward a phylogenetic classification of the Ephemeroptera a commentary on Systematics *Ann Entomol Soc Amer* **84** 343–360

McCafferty W P & Edmunds G F 1979 The higher classification of the Ephemeroptera and its evolutionary basis *Ann Entomol Soc Amer* **72** 5–12

Mol A W M 1978 Notes of chromosomes of some West European Ephemeroptera *Chromosome Inform Serv* **24** 10–12

Pfau H K 1986 Untersuchungen zur Konstruktion, Funktion and Evolution des Flugapparates der Libellen (Insecta, Odonata) *Tijdrschr Entomol* **129** 35–123

Riek E F & Kukalova-Peck J 1984 A new interpretation of dragonfly wing venation based upon early upper Upper Carboniferous fossils from Argentina (Insecta, Odonatoidea) and basic character states in pterygote wings *Canad J Zool* **62** 1150–1166

Soldan T 1979a The structure and development of the male internal reproductive organs in six European species of Ephemeroptera *Acta Entomol Bohemoslov* **76** 22–33

Soldan T 1979b A comparative study of spermatozoa of some Central European Ephemeroptera *Acta Entomol Bohemoslov* **76** 223-230

Soldan T 1979c The structure and development of the female internal reproductive organs in six European species of Ephemeroptera *Acta Entomol Bohemoslov* **76** 353–365

Soldan T 1997 The Ephemeroptera – whose sister-group are they? Pp 514–519 In Landolt P & Sartori M (eds) *Ephemeroptera & Plecoptera Biology – Ecology – Systematics* Fribourg Mauron+Tinguely & Lachat, 569 pp

Traut W 1976 Pachytene mapping in the female silkworm, Bombyx mori L (Lepidoptera) *Chromosoma* **58** 275–284

Wheeler W C 1989 The systematics of insect ribosomal DNA In Fernholm B (ed) *The Hierarchy of Life* Amsterdam Elsevier, 499 pp

Wolf E 1946 Chromosomenuntersuchungen an Insekten *Ztschr Naturforscher* **1** 108–109

Wolf E 1960 Zur Karyologie der Eireifung und Furschung bei Cloeon dipterum L (Bengtsson) (Ephemerida, Baetidae) *Biol Zbl* **79** 153–198

INSTRUCTIONS TO AUTHORS

Acta Societatis Zoologicae Bohemicae publishes in English, original papers on general, applied and systematic zoology, biographies and book reviews Papers by members of the Czech Zoological Society are prefered It is understood that manuscripts submitted are not offered to any other journal for prior or simultaneous publication

Authors of taxonomic papers must respect the articles of International Code of Zoological Nomenclature (Fourth Edition, 1999) and observe its recommendations The manuscript including footenotes, references and tables, must be typed with double spacing (30 lines per page) on side A4 paper (210 mm × 297 mm), in duplicate and should be not longer than 30 pages Pages must be numbered throughout the manuscript Final version (corrected as requested referees and editorial board) is preferably accepted on IBM PC – compatible 5 25"or 3 5" diskette

Heading Title of paper, full name(s) of author(s), place of work with full address – on separate line

Abstract summarizing consisely the contents of the paper and indicating the relevance of the work, should not *exceed 20 type-writen lines*

Key words Select a set (one or two lines) of key words (index terms)

References Within the text – Dryden (1968) (Lattin 1967), Kummari & Nair (1967), Tamiro et al (1970), the full citation should be given in the list of references Under the References authors should be cited in full followed by abbrevitations of periodical in accordance with The World List of Scientific Periodicals, 4th edition, London Butterworths (1964–1965) The number is to be given (in parentheses) only when individual numbers are paginated independently (see example b) References to papers published in languages other than the major ones, or printed in characters other than Latin, should be content English translation, with an appropriate note at the end (see examples e, f, g, h)

Examples

(a) Dryden G L 1968 Growth and development of Suncus murinus on Guam J Mammal 49 51–62

(b) Lonberg E & Gustavson C 1937 Contribution to the life history of the stripped wrasse Ark Zool 29(7) 1–16

(c) Lattin G de 1967 Grundriss der Zoogeographie Jena Fischer Verlag, 602 pp

(d) Makin D 1989 The status of bats in Israel Pp 403–408 In Hanak V , Horaček I & Gaisler J (eds) European Bat Research 1987 Praha Charles Univ Press, 718 pp

(e) Schornikov E I 1969 A new family of Ostracoda from the supralitoral zone of Kuril Islands Zool Zh 48 494–498 (in Russian, Engl abstr)

(f) Nikolajev G V 1987 Plastinchatousye zhuki (Coleoptera, Scarabaeoidea) Kazakhstana i Srednei Azii [Scarabaeoidaea (Coleoptera) of Kazakhstan and Central Asia] Alma-Ata Izd Nauka KazSSR 232 pp (in Russian)

Nikolaev G V 1987 Plastinčatousye žuki (Coleoptera, Scarabaeoidaea) Kazahstana i Srednej Azii [Scarabaeoidaea (Coleoptera) of Kazakhstan and Central Asia] Alma-Ata Izd Nauka KazSSR, 232 pp (in Russian)

(h) Lekeš V 1993 [Macrolepidoptera of the Polabi lowland] Polabska Příroda 4 19–20 (in Czech)

Illustrations and their captions or legends must form a separate unit Clear technically perfect line drawings and photographs (black-white, glossy) are accepted The original drawing and photograph (one set) should be more than twice as large as when printed and preferably into blocks or plates so that the blocks of drawings or photographs may be uniformly reproduced over the age with the journal Legends to the illustrations should be supplied on a separate sheet of paper References to illustrations and tables in the text Fig 1, Figs 1–2 Plate 1, Fig 1 (for photographic plates), Table 1, Tab 1, Tabs 1–2

Tables including headings and explanations should be on separate sheet of paper, numbered consequently with Arabic numerals

Marking in the manuscript (in light pencil, not in ink or type written) In the text Latin taxa up to generic level – with wavy underling (italics) In the References names of periodicals (not the Latin names of taxa) with wavy underling

Proofs will be sent to authors One houndred reprints are supplied free of charge Manuscripts of published papers, diskettes and originals of illustrations are not returned unless return requested

Address of the editorial office Acta Soc Zool Bohem , Dr David Kral, Viničná 7, CZ-128 00 Praha 2, Czech Republic

Acta Soc Zool Bohem **64** 446, 2000
ISSN 1211-376X

BOOK REVIEW

ROMOSER W S & STOFFOLANO Jr J G **The Science of Entomology** Fourth updated and substantially expanded edition WCB/McGraw-Hill, a Division of the McGraw-Hill Companies, Boston, Burr Ridge, Dubuque, Madison, New York, San Francisco, St Louis, 1998 XIV+605 pages *Format 210×275 mm Hard cover Price* USD 103 00 ISBN 0-697-22848-7

The authors are affiliated with Universities in Ohio and Massachusetts It is accentuated in the preface, that in adaptive diversity and in number of individuals, the insects are among the most successful of all organisms Thus entomology is an important applied science as well as a major area of basic biology The publication is divided into five parts and includes 18 chapters The initial chapter summarizes the impact of positive and negative activities of insects on health and agriculture and presents an overview of various publication and electronic information sources related to entomology **Part One** offers a comprehensive treatise of **Structure and Function** It is the most extensive part while presenting close to one half of the page extents of this book It begins with detailed treatment of the integumentary system Further on, delineated are the skeletal structures, the general insect body plan and its specific morphological modifications Next chapter examines the nervous, glandular and muscular systems The following chapter deals with alimentary, circulatory, ventilatory and excretory systems In explicit detail, the authors describe particular parts and functions of the insect digestive canal In the framework of the circulatory system are comprised the dorsal vessel and accessory pumps, along with sinuses and diaphragms, regulatory mechanisms and general characteristics of the haemolymph Next coming textual parts illuminate the structure of ventilatory tubules and respiratory processes, further on the excretory system The chapter elucidating reproduction and development takes a look at the reproductive system and gametogenesis, at seminal transfer, fertilization and sex, embryogenesis and postembryogenic morphogenesis In the context of sensory mechanisms are discussed the morphology and functions of sense organs (sensillae) Finally are analysed the terrestrial, aquatic and aerial ways of locomotion, and miscellaneous aspects of behaviour **Part Two** is concerned with **Insects and Their Environment** while surveying insect populations and their interactions with physical, chemical and biotic environmental factors Special attention is given to the relationship between insects and plants **Part Three** introduced under the heading **Unity and Diversity** ensures coverage of insect classification and evolution Discussed is the place of basic systematics among the other specialties in the biological science – a topic that is often neglected in the age of molecular biology Subsequent chapters give an overview of the insect orders and families Descriptions of particular orders of apterygote and pterygote insects along with selected major families are constructed within the framework embracing the body characteristics Moreover, provided is information regarding their medical, economic, and ecological significance **Part Four** constitutes a highlight of **Applied Entomology** Insects are explored here from the viewpoint of beneficial activities, as organisms for fundamental biological research, and their role in nature Insects are mentioned also as food for humans and domestic animals From the viewpoint of harmful activities delineated are diverse kinds of injury to growing plants, destruction of stored products, household goods and structural materials, the ways of attack humans and the animals and the insects as the causative agents of disease and dyscomfort Subsequent chapters focus on conservation and biodiversity of insects, on insect control arsenal while incorporating biological, genetic, ecological, microbial and chemical tools of control The reader can find here an overview of insecticides This part concludes with a chapter providing access to the integrated pest management in agroecosystems **Part Five** centres attention upon **The Modern Interface** – it has been newly introduced to this edition and acquaints the reader with rapidly evolving procedural techniques of molecular biology Procedures of molecular biology have found application in the study of insect evolutionary relationships, in insect identification and embryogenesis in the study of molecular basis of insecticide resistance, in identification of arthropod-borne pathogens, in genetic manipulation of insects and more An **Appendix A** compiled by F A Horodyski encompasses identification keys to major insect orders and families The volume is concluded with a glossary of terms relevant to entomology This authoritative and readable textbook takes fundamental, state-of-the-art approach towards general entomology aimed at advanced students and professional entomologists as well as at parasitologists of various profiles It is profusely illustrated by a wealth of figures numbered separately in each chapter and composed of schematic line drawings and photographs In addition textual information is supported by abundant summary-type tables and boxes Each chapter is supplied with an extensive list of references In this way, the volume presents a thorough synopsis both of classic and most actual entomological literature, embracing original scientific reports, monographs and textbooks

Jindřich Jira

CONTENTS

Articles

Benda P & Tsytsulina K. A · Taxonomic revision of *Myotis mystacinus* group (Mammalia· Chiroptera) in the western Palearctic 331

Hůrka K & Řezáč M. *Metajapyx braueri* (Hexapoda: Japygina· Japygidae) in Prague, Bohemia 399

Kejval Z.: Revisional notes on the Palaearctic *Formicomus* (Coleoptera Anthicidae) 403

Mlikovsky J & Göhlich U. B.· A new wood-hoopoe (Aves: Phoeniculidae) from the early Miocene of Germany and France 419

Skuhrava M. & Hinz H. L. *Rhopalomyia tripleurospermi* sp n (Diptera. Cecidomyiidae), a new gall midge species on *Tripleurospermum perforatum* (Asteraceae. Anthemideae) in Europe, and a biological control agent in Canada 425

Soldan T & Putz M Karyotypes of some Central European mayflies (Ephemeroptera) and their contribution to phylogeny of the order 437

Book review

Mehlhorn H. & Piekarski G · Grundriss der Parasitenkunde. Parasiten des Menschen und der Nutztiere – by J. Jíra 402

Romoser W. S. & Stoffolano Jr. J G . The Science of Entomology – by J Jíra 446

Podávání novinových zásilek povoleno Ředitelstvím pošt v Praze č. j. NP 1176/1994 ze dne 13. 6. 1994.

ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE

Vol. 64 – 2000

Editorial Board
Karel Hůrka (Editor in Chief), David Král (Executive Editor), Petr Benda, Jan Buchar,
Ivo Hodek, Alois Honěk, Jaroslav Hrbáček, Vojtěch Jarošík, František Moravec,
Josef Rusek, Jiří Vávra, Jan Zima

Czech Zoological Society
Praha

ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE

Vol 64 – 2000, No 1–4

CONTENTS

Articles

Angelini F & Švec Z New species of the genera *Cyrtusa*, *Pseudcolenis*, *Cyrtoplastus* and *Agathidium* (Coleoptera Leiodidae Leiodinae) from China 119

Benda P Record of *Hipposideros doriae* (Mammalia Chiroptera) from Sabah (East Malaysia) and remarks to species status of *Hipposideros sabanus* 143

Benda P & Tsytsulina K A Taxonomic revision of *Myotis mystacinus* group (Mammalia Chiroptera) in the western Palearctic 331

Beran L First record of *Corbicula fluminea* (Mollusca Bivalvia) in the Czech Republic 1

Bocak L A revision of the genus *Microtrichalus* from Sumatra, with notes on Oriental and Australian species (Coleoptera Lycidae) 3

Bocakova M Review of the genus *Libnetis* from China with descriptions of several species from Thailand (Coleoptera Lycidae) 223

Frynta D, Kratochvil L, Moravec J, Benda P, Dandova R, Kaftan M, Klosova K, Mikulova P, Nová P & Schwarzova L Amphibians and reptiles recently recorded in Libya 17

Haněl L Microgradient changes of soil nematodes (Nematoda) in litter and moss-lichen transects in spruce and beech forests 27

Hubert J Seasonal changes of abundance, sex ratio and egg production of *Scheloribates laevigatus* (Acari Oribatida) in the soil of a meadow in the Czech Republic 37

Hurka K & Řezáč M *Metajapyx braueri* (Hexapoda Japygina Japygidae) in Prague, Bohemia 399

Kejval Z Revisional notes on the Palaearctic *Formicomus* (Coleoptera Anthicidae) 403

Kovařík F First reports of *Liocheles nigripes* from Indonesia and Malaysia and *Hormiops davidovi* from Malaysia (Scorpiones Ischnuridae) 57

Kovařík F Revision of family Scorpiopidae (Scorpiones), with descriptions of six new species 153

Kovařík F Revision of *Babycurus* with descriptions of three new species (Scorpiones Buthidae) 235

Kral D A review of Chinese *Aphodius* species (Coleoptera Scarabaeidae) Part 2 revision of the subgenus *Brachiaphodius* 65

Kral K & Rejsek J *Synapsis naxiorum* sp n from Yunnan (Coleoptera Scarabaeidae) 267

Mlikovsky J Early Miocene pratincoles (Aves Glareolidae) from Dolnice, Czech Republic 93

Mlikovsky J & Gohlich U B A new wood-hoopoe (Aves Phoeniculidae) from the early Miocene of Germany and France 419

Moravec F Review of capillariid and trichosomoidid nematodes from mammals in the Czech Republic and the Slovak Republic 271

Pižl V An addition to the earthworm fauna of the Czech Republic 203

Skuhrava M & Hinz H L *Rhopalomyia tripleurospermi* sp n (Diptera Cecidomyiidae), a new gall midge species on *Tripleurospermum perforatum* (Asteraceae Anthemideae) in Europe, and a biological control agent in Canada 425

Soldan T. & Putz M.: Karyotypes of some Central European mayflies (Ephemeroptera) and their contribution to phylogeny of the order 437

Švec Z.: Chinese species of the genus *Leiodes* (Coleoptera: Leiodidae: Leiodinae) 97

Tkalců B.: New palaearctic species of the genera *Anthocopa* and *Hoplitis* (Hymenoptera: Apoidea: Megachilidae) 305

Vitner J.: Variability of behavior in the larvae of *Aphodius* (*Colobopterus*) *erraticus* (Coleoptera: Scarabaeidae) 115

Vitner J.: Field observations on the biology of *Copris lunaris* (Coleoptera: Scarabaeidae) 209

Obituary

Nedvidek J. & L. Janský L.: In memoriam Professor Alexej Romanovský (January 13, 1932 – July 26, 1999) 217

Book reviews

Clements A. N.: The Biology of Mosquitoes. Volume 2. Sensory Reception and Behaviour – by J. Jíra 114

Harrison F. W., Locke M. (vol. eds.): Insecta. In: Harrison F. W. (treatise ed.): Microscopic Anatomy of Invertebrates – by J. Jíra 202

Freedman D. O. (volume editor). Immunopathogenetic Aspects of Disease Induced by Helminth Parasites – by J. Jíra 208

Fuller E.: The Great Auk – by J. Chalupský 266

Liew F. Y., Cox F. E. G., volume editors: Immunology of Intracellular Parasitism – by J. Jira 142

Mehlhorn H. & Piekarski G.: Grundriss der Parasitenkunde. Parasiten des Menschen und der Nutztiere – by J. Jíra 402

Roberts L. S., Janovy Jr J.: Gerald D. Schmidt & Larry S. Roberts' Foundations of Parasitology – by J. Jira 216

Romoser W. S. & Stoffolano Jr. J. G.: The Science of Entomology – by J. Jíra 446

Data of appearance of the issues

1 – April 7, 2000
2 – July 7, 2000
3 – October 31, 2000
4 – December 29, 2000